

FUNDAMENTAL

ANIMAL PHYSIOLOGY

[For Graduate, Honours and Post Graduate
Students of Indian Universities]

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FOREWORD

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physiology.

As a matter of fact, both the classical books and the academic teaching in physiology are restricted usually to one or the other of these two aspects of the field of animal physiology.

An
parative
ones, through invertebrates and lower vertebrates upto mammals including man.

acquisition of more and more specialised and complex systems annexed to the cellular metabolism, such as circulatory, respiratory, digestive, excretory; and corelatively to the development of fine regulatory mechanism including the central nervous system and systems allow an
iment and adjust-

On the other hand the comparative approach permits to trace
associated to homoeothermal and homoeosmotic adaptation in birds and mammals.

Such a basic understanding in comparative and general physiology should be of high profit to the graduate and post graduate students before they specialise in some definite branch of zoology. We must, therefore, be very grateful to professors S. M. Das and S. A. Haq for their outstanding attempt to present here a concise and comprehensive textbook of animal physiology with illustrations, which will be of greatest help to students as well as to teachers and even to specialist physiologists who may not be familiar with the comparative approach to physiology.

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PREFACE

The teaching of biology today is not the same as it was even ten years ago. The immense pile of data coming on top of one another every year, as new discoveries pour in, would double the content of our teaching in ten years. It would, therefore, be an impossible task to keep pace with today's scientific changes in its character. The task of adequate presentation of the dynamic state of modern physiology.

It is vitally important that students of Zoology at college and University level should be able to visualize and animal as a com-

REVIEW

There are only a handful of books available on general and comparative physiology in India. Even these are either too abstruse and elaborate for our students, or hardly cover the curricula and courses of study. It is hoped that the present book will serve as a basic material for medical students, graduate and honours students of biology, and even those post graduate students who specialize in a particular discipline of Zoology other than physiology.

The author will be thankful for any addenda or corrigenda that teachers of Zoology and Physiology may suggest for improvement of the future editions. Some shortcomings have to be overlooked due to the concise presentation of vast material that constitutes Animal Physiology.

S. M. Das

S. A. Haq

A centipede was happy till,
one day a toad in fun
said ; pray which leg moves after which ?
This raised her doubts to such a pitch,
she fell exhausted in the ditch ;
not knowing how to run .

(Cerebral Inhibition)
Sir Ray Lankester

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Chapter I

LOCOMOTION AND MOVEMENTS (EFFECTOR SYSTEM)

Locomotion and movements of an animal are produced by effectors, which are the parts by which animals respond to changes in the environment. An effector system may consist of individual cells, collection of cells or parts of cells by the use of which the animal changes its own position or its own body parts. Effectors cause movement by stimulation either through the nervous system or by hormones. Cilia, flagella, pseudopodia as well as muscles are all concerned with movements. The action of all these structures is based on alternate contraction and extension (e.g., *Vorticella*) or contraction and relaxation (e.g., earthworm and most higher animals). The basic chemistry of these changes is

INVERTEBRATES

CILIA

moto

move

are present on the surface of the body in some coelenterates, turbellarians, rotifers, nemertines and some snails, e.g., *Nassarius*. Cilia are absent in nematodes and molluscs. Although present in the gills of lamellibranchs, gastropods and bivalves, they do not cause movement or locomotion of the animal.

feeding and respiratory currents, filtering of food particles and conveying them to the oral opening through special ciliary tracts. Ciliary movement is important for the transport of food in the alimentary canal of some echinoderms molluscs, *etc.*, and has a cleaning role, as the ciliated epithelium of frog's mouth, and the cilia of the respiratory tract in mammals. Cilia can only function in an aquatic medium.

The **ultra structure** has been elucidated with the aid of electron microscope studies for the cilia of the protozoans *Paramecium*, *Cyclidium*, *Ephelota* as also for the gill cilia of *Mytilus*. All cilia show a uniformity of structure and organization. A cilium is composed of a plasma membrane sheath enclosing a central filament, surrounding which are a number of peripheral filaments. At its base of attachment there is usually a basal plate and an anchoring process called the rootlet. The peripheral filaments, often called the outer fibres, are about twice as thick as the axial

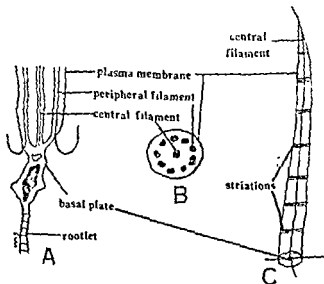


Fig. 1. Structure of a cilium as seen under electron microscope.
A. Longitudinal section of basal plate of cilium in *Paramecium*.
B. Transverse section of cilium of *Paramecium*.
C. Entire cilium of *Cyclidium*.

fibres (Fig. 1). Cilia often unite or fuse to form compound

organelles, such as the cirri of *Stylonychia*. They may form a membranelle at the adoral region of some ciliates (e.g., *Paramecium*). It is remarkable that the component cilia in these organelles beat independently of each other when separated by micro-dissection; if reunited they show the same co-ordinated activity of undulatory movement.

CILIARY MOVEMENT

Ciliary movement can be differentiated into four types:

- (1) The simplest is a pendular movement flexing to and fro only at its base (e.g., frog pharynx and *Stylonychia*);
- (2) Bending at
up to the 1
the cilium straightens from base to tip in the reverse direction (e.g., cilia of Lamellibranch gills);
- (3)
- (4)

directional locomotion. The cilia beat in metachronous waves (Fig. 2) as a paddy field affected by a breeze (*Opalina*). There may, however, be complex ciliary activity involving a combination of 1 and 2 or 3 and 4.



Fig. 2. Cilia of *Opalina* beating in metachronous waves.

Theory of Ciliary Movement.—Up to 1910 it was assumed that the moving force occurs in the cell body proper, while the cilia act only passively. Schafer, Heidenhain (1911), however, postulated that the cilium itself contains actively contractile elements responsible for the movements. This is supported by the factual observation that the waves passing out along a cilium show no reduction in amplitude. A reduction in amplitude would certainly be expected if the contraction occurred only in the cell-body.

Like muscular activity, the rate of ciliary movement increases with the concentration of oxygen, the rate of consumption of oxygen increases in the ciliary activity. The cilia in paramecium stop beating within a few seconds in an oxygen lacking medium. Adrenalin and low concentrations of acetylcholine increase the rate of beat of cilia as happens in muscular activity. Absence of calcium ions stop ciliary beating without affecting oxygen consumption.

FLAGELLA

The structure of a flagellum is about the same as that of a cilium; only it is much longer and stouter. The flagellum, which

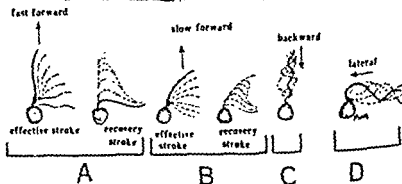


FIG. 3. Flagellar locomotion in *Alveolar* arrows show the direction of locomotion.

- A. Fast forward.
- B. Slow forward.
- C. Backward.
- D. Lateral.

may be single or multiple in a flagellate or a cell, is a vibratile structure capable of rapid pendular movement from a forwardly

directed position to a position at right angles to the direction of locomotion, the effective stroke being backwards as in an oar. In rapid forward movement the effective stroke is a rapid pendular movement, the recovery stroke being typical flexural recovery. In slow forward movement the flagellar sweep may be reduced to about half the amplitude. Backward movement is brought about by undulatory activity of the flagellum, with the wave passing from base to the tip of the organelle. In lateral progression (*Euglena*, *Monas*), the flagellum is kept flexed at about 90° opposite to the direction of movement, performing undulating movement (Fig. 3).

SPEED OF CILIARY AND FLAGELLAR LOCOMOTION

The speed of locomotion of *Paramecium* is of the order of 1 mm/sec; while particles on ciliated epithelium in higher animals move at more than 4 mm/sec. *Euglena* moves at about 0.2 mm/sec; while *Volvox* when free swimming has 1 mm/second speed.

PSEUDOPODIA

Pseudopodia are found in protozoan animals, archaeocytes of sponges, endodermal cells of coelenterates, phagocytes of most

axial filamented axopodia (e.g., *Heliozoa*); and (4) fine anastomosing rhizopodia (e.g., *Foraminifera*), some of which become reticulate and are called **reticulopodia**.

dia cause **amoeboid**

1) flowing as a thin liquid

(i.e., ill defined pseudo-

podia as in *Mycetozoa*); (2) one or more lobose pseudopodia formed causing a rolling movement (as in *Amoeba proteus*); (3) radiating pseudopodia formed, suspending the animal in water (as in *Amoeba radiosa*); (4) the pseudopodia become attached by the tips and then contract drawing up the animal (*Diffugia* and *Polystomella*); (5) wheeling action caused by successive axopodia being put out, attached and contracted, so that animal rolls on a succession of spokes (e.g., *Heliozoa*).

Chemical Basis of Amoeboid Movement.—*Amoeba* consists of three layers: (1) a thin plasmalemma on the outside; (2) a viscous plasmagel sheath under it; and (3) a fluid plasmasol internally in which the nucleus is suspended. Locomotion in amoeba according to **Mast** is effected in four steps: (1) attachment to substratum; (2) solation of plasmagel at the temporary posterior end, (3) streaming of plasmasol towards the temporary anterior end; and (4) formation of pseudopodium with gelation of plasmasol. The sol-gel balance is thus maintained by the same amount of gelation at anterior end as solation at posterior end. Initiation of movement in a resting amoeba occurs at posterior end by ATP action. This is proved by injection of ATP at posterior end causing solation of the gel and faster movement of the amoeba. If injected at the anterior end the amoeba reverses its movement.

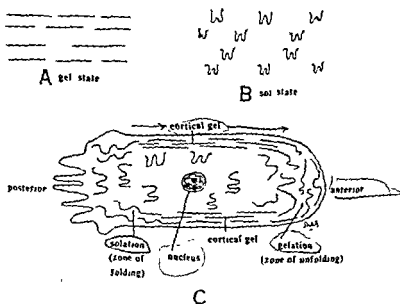


Fig. 4. A sol-gel balance in amoeboid movement

parts of an

The actual process of solation and gelation has been explained

viscous in the gel state (fig. 4).

Physical Basis of Amoeboid Locomotion.—In a resting Amoeba there is always a zone of maximum resistance, a zone of medium resistance and a zone of minimum resistance. With the starting of solation the contraction is at posterior end, which is the zone of maximum resistance. The sol thus flows forward towards the minimum resistant anterior end, since the sides have medium

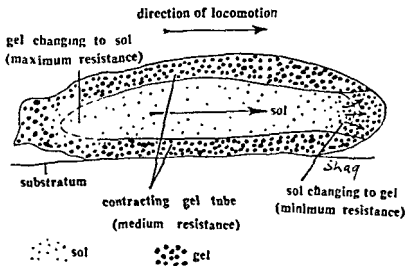


Fig. 5. Amoeboid locomotion (solation/gelation resistance).

resistance (Fig. 5). It has been found that the flowing of sol into the pseudopodium is through one of three ways: (1) by a number of small rupture openings in the gel sheath, (2) by a few large openings in the gel sheath, and (3) in fast movement by one large rupture in gel sheath at anterior end, as in *Amoeba limax*.

Theories of Amoeboid Movement.—Omitting the theories of Schultz (1861), Schulz (1875) and Dillinger (1905) postulating protoplasm contractility, streaming contraction and walking theories, respectively, the recent theories are:

(1) Sole-gel theory of Hyman (1917) and Mast (1932),

(2) Acid secretion and water absorption (1923) theory of Pantin (1923); and

(3) Molecular folding and unfolding theory of Goldacre and Lorch.—Electron microscopy reveals filaments resembling myofibril filaments in the gel of *A. proteus*. Similarly the axopodia of heliozoa and radioloria are highly contractile and fibrillar.

MUSCLE

Most muscles originate from the mesoderm in all triploblastic animals. A Muscle consists of a number of individual elongated

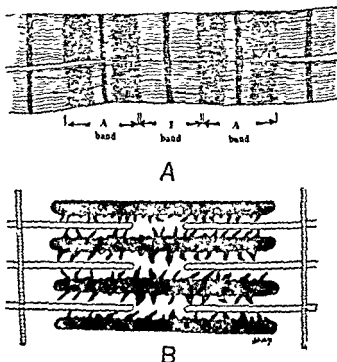


Fig 6 Ultra-structure of a striated muscle (fibres as seen under an electron microscope).
A. Structure.
B. Mechanism of action.

muscle fibres which have the property of contracting in length and expanding in girth when stimulated. Thus the volume of contracted and relaxed muscle fibres remains the same. Muscle

fibres are made up of a number of myofibrils, which consist largely of a protein called myosin. The myofibrils are embedded in a
proteins actin and myosin. All these together form the contrac-
n alone is able to
artificial fibrils of
are added water,
actomyosin fibrils
 contract.

In the process of contraction ATP is changed into ADP
(Adenosine diphosphate).

A resting muscle contains: adenosine triphosphate—ATP, phosphocreatine—PC, and glycogen. With contraction each undergoes chemical change and releases energy. The actual chemical process of energy release is as follows:

- (1) ATP is changed to ADP; and this in turn is converted into AMP (Adenosine monophosphate);
- (2) PC (phosphocreatine) is broken down into creatine and phosphate;
- (3) Glycogen is converted into lactic acid;
- (4) Lactic acid is removed from the tissues by oxidation.

If it is not removed the muscle remains in a contracted state causing cramps.

The energy released by the first three reactions is utilized as follows:

- (1) Breakdown of ATP provides energy for muscular contraction.
- (2) Breakdown of PC supplies energy to re-synthesize ATP.
- (3) Breakdown of glycogen into lactic acid provide energy for reforming PC from phosphate and creatine.

- (4) Oxygen reacts with about one-fifth of lactic acid providing energy for reversion of the remaining four-fifth of lactic acid to glycogen.

It may be added that breakdown of both ATP and PC is by hydrolysis (addition of water) and involves no oxidation. Hence reduction of ATP and PC can take place even in anaerobic condition (i.e. in absence of oxygen). On the other hand reversion of lactic acid to glycogen or the removal of lactic acid as CO_2 is aerobic. The activator initiating contraction in a muscle is always ATP.

All muscles contract to perform work. A synthesized actomyosin fibril can contract and lift up to one thousand times its own weight; and this is exactly what happens in skeletal muscles. About 30% of the energy is used for work, while the balance produces heat in the body. About four-fifth of our body heat is derived from this source. After continuous work every muscle undergoes fatigue, which is the inability to continue contraction. This is caused by the accumulation of lactic acid and depletion of glycogen and ATP.

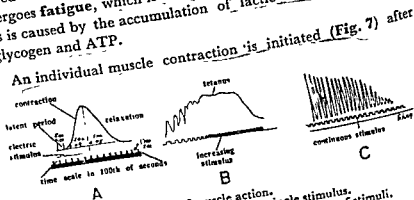


Fig. 7. Kymograph Records of muscle action.
A. Contraction and relaxation by a single stimulus.
B. Tetanus contraction by increasing frequency of stimuli.
C. Fatigue due to continued application of stimuli.

about 0.01 second of the application of the stimulus. This is known as the **latent period**. In the next phase, i.e. the **period of relaxation**, lasting about 0.05 second, the muscle returns to its original length and physiological state. If repeated stimuli are applied at close intervals, the muscle cannot relax completely to its

original length. This state is called clonus. If the muscle remains in this state of continued contraction it is called tetanus. Certain muscles of the body are always in a contracted condition, providing the feel of a firm muscle. This firmness of a muscle is called tonus and helps to keep the body in a particular posture while sitting, standing or at work. Tonus continues without fatigue, because some fibres of a muscle are contracted while others are relaxed and resting, there being rotation of their roles. Without tonus particular postures of work would be impossible as in poliomyelitis (polio) atonic muscles, which remain flabby (also hypertonic condition obtains in epilepsy and tetanus diseases).

Muscle bands function in groups called motor units, each of which is controlled by one motor neurone, e.g. human eye muscles have 2-6 fibres per motor unit; a cat's leg up to 165 and other leg muscles up to 600 such units. Excepting for cardiac muscles contraction in all muscles, whether striated or not is activated by motor-nerve impulses as follows:

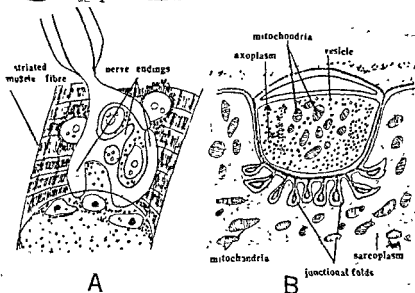


Fig 8. A. Motor end plate in striated muscle fibre of a mammal.
B. T. S. of one branch of motor end-plate of mammal. (After Prosser and Brown).

1. Nerve impulse → chemical transmitter (acetylcholine) →

end plate potential \rightarrow muscle impulse \rightarrow activation of myofibrils (Fig. 8); or

2. Nerve impulse \rightarrow chemical transmitter (acetylcholine) \rightarrow junctional potential \rightarrow activation of myofibrils (Fig. 9).

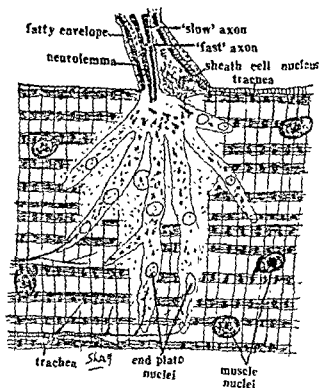


Fig. 9. Motor end-plate in locust leg muscle (After Prosser and Brown).

A motor unit is thus activated to contract either fully or not at all. This is called the **all or none principle**.

INVERTEBRATES

Origin and Organisation of Muscles.—Muscles may be said to have originated in protozoa, where contractile tissue is present as myonemes and myofibrils (Fig. 10). In the *Zoothamnium* (Fig. 11) there is a neuro-fibrillar apparatus, nerve-line system, (Fig. 11). In coelenterates the muscle processes of ectodermal cells are arranged in

longitudinal as well as circular sets, which contract alternately and

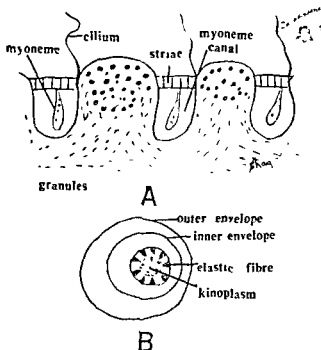


Fig. 10. A. T. S. of ectoplasm of *Steutor*.
B. T. S. of stalk of *Zoothamnium*.

have opposite actions. When longitudinal muscles contract the

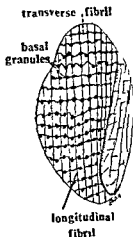


Fig. 11. Silver-line system (Kino-motor apparatus) of *Ancistruma* (ciliate).

tubular structure shortens and thickens and when the circular muscles contract the body lengthens and narrows (e.g. *Hydra*, Earthworm) (Fig. 12). In the intestines of vertebrates the same

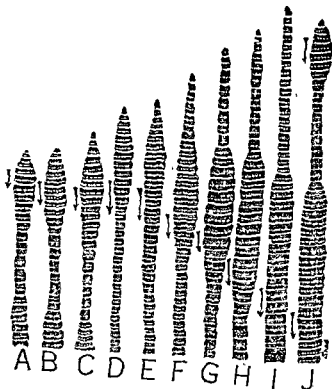


Fig. 12. A to I.—Locomotion in Earthworm (wave indicated by arrows).
J.—A new contraction wave starts at the anterior end. (The animal elongates and moves anteriorly by contraction of circular muscles; when longitudinal muscles contract the body shortens and thickens, anchoring to the ground).

alternate coordinated contractions of circular and longitudinal muscles pass as a wave along the tube, known as peristalsis, which forces the contents in one direction. Another type of circular muscles is sphincter which closes off a tubular organ, e.g. the pyloric sphincter and anal sphincter.

In higher animals, locomotor muscles have usually two attachments, one the spot of origin and other the spot of insertion.

Usually two types of such muscles are present, antagonising each other and called **antagonistic muscles**. In arthropods the skeleton is external (exoskeleton) and muscles internal, while in vertebrates straightening or extension of a joint is by **extensor**

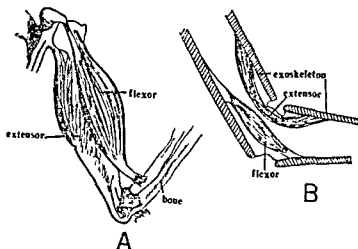


Fig. 13. Typical arrangement of opposed muscles.
A. In the endoskeleton of a vertebrate.
B. In the exoskeleton of an arthropod.

muscles (Fig. 13). This can be easily seen in the action of biceps

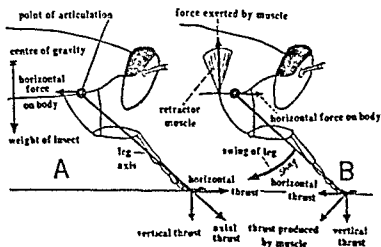


Fig. 14. Mechanism of walking in an insect.
A. Leg used as a strut.
B. Leg used as a lever. (After Chapman)

and triceps, contraction of the biceps (flexor) bending the elbow, and contraction of the triceps (extensor) straightening the elbow; (i.e. when flexor contracts the extensor relaxes and vice versa).

Muscle Function in Locomotion.—Besides the alternate contraction of circular and longitudinal muscles for locomotion, already seen in earthworm, and the flexion and extension of arthropod joints by opposed muscles (Fig. 14), insect flight offers a challenge in the physiology of locomotion (Fig. 15). This is so because the

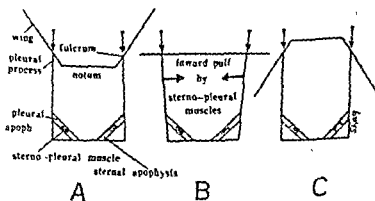


Fig. 15. A cross section of insect thorax, illustrating wing movement.
 A. Wings stable in the 'up position'.
 B. Unstable position due to inward pull by sternopleural muscles.
 C. Wings stable in the 'down position'. (After Chapman)

minimum time required for a complete cycle of contraction and relaxation in a muscle, receiving a single nerve impulse is of the order of 15 to 20 msec (1 msec=one thousandth of a second). At the level of this rate of contraction and relaxation only 50 to 70 complete cycles could occur in one second. But the wing beat of some insects, such as mosquitoes and bees may be several hundred cycles per second, which would mean 3 to 4 wing movements for one impulse. This however is not physiologically possible. The explanation lies in the fact that in a flying insect, the wings, wing muscles and the thorax form an elastic system which exhibits

resonant oscillating vibrations. The much slower nerve impulses only serve to reinforce these oscillations (Fig. 16).

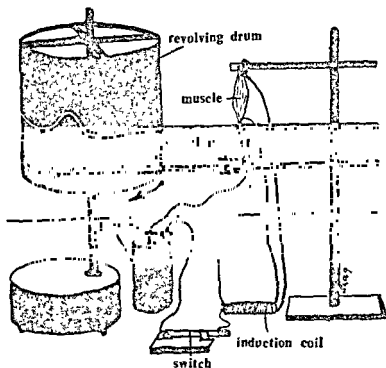


Fig. 16. A kymograph showing recording of muscle contraction.

VERTEBRATES

Fishes are efficient swimmers in the resistant medium of some force. The ves of contraction each wave striking the water postero-laterally; the resultant force of the two sides causing the forward movement. As explained by James Gray large sweeping movements of the tail and caudal fin help in fast locomotion as the resultant force (Fig. 18) propels the fish forwards.

In *Amphibia* both aquatic (natatory), terrestrial walking (ambulatory) and terrestrial jumping (saltatorial) locomotion is

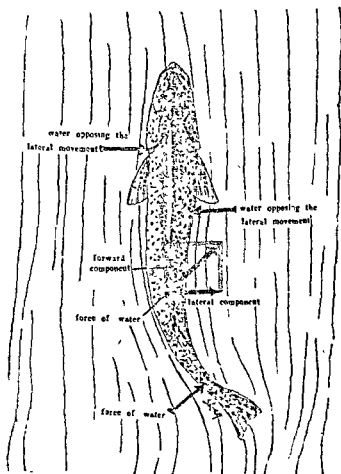


Fig. 18. The lines of force in fish-locomotion in water.
(After Gray)

present. The hind-limbs of the frog are much longer than the fore-limbs, the elongation being due not only to long thigh and shank but a disproportionate elongation of the ankle. Both in swimming and jumping it is the hind-limbs which are straightened out and a powerful forward thrust is obtained against the water (swimming) and against the substratum (jumping), the webbing of the foot adding to the thrust in water.

The toads and the salamanders, however show walking or crawling movements. The fore and hind-limbs of the same side being extended while those of the opposite side remain flexed (Fig. 19).



Fig. 19. Stages in the walking locomotion of toad (arrows indicate the flexion and extension of limbs).
(modified after Gray)

fish
well
vertebral column which is axially situated in the fishes, becomes totally dorsal in reptiles, so that most of the body hangs below the chair of vertebrae. As in the toad and salamanders, the limbs protrude the body by the same alternate extension, and flexion of the limbs on the opposite sides.

Birds evolved as flying machines through the evolution of feathers under two prime requirements of high power and low weight. The body of the birds is streamlined and have

to the wrist is adapted to give the bird a lift force; while the outer half from the wrist to the wing tip is for propulsion (driving force).

the birds have special equipment for steering and balancing. It steers by turning its tail up, down or sideways, spreading the tail wide to give added lift when required. Balancing is done by means of its wings by increasing the lift of the wing on its tipping side and restoring itself to an even keel (Fig. 21).

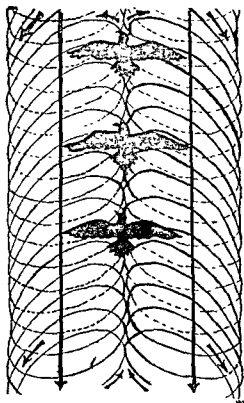


Fig. 21. Soaring of a bird.
(after Storer)

Birds show three types of flight in the main :—

- (1) *Flapping* flight (already explained) ;
- (2) *Soaring* flight ; and
- (3) *Gliding* (coasting) flight.

Soaring flight can be seen in the flying eagle and vulture in land, and the albatross over the sea, During soaring the bird

risers in the air sailing on motionless wings. This is due to the bird riding a rising current of air, the air ascending faster than the bird. Ascending air currents are caused by a deflecting hill-side, or by large ocean waves in the sea. Another cause of fast ascending air current is thermal, when air is heated by the sun over land tracts or sea. The upward air current has the structure of columns of air packed together. These columns have air rotating around their axils. The bird thus rides an up draught of air between two counter rotating cylinders of air. This is so specially with the large albatross of the sea which moves effortlessly hundreds of miles after an ocean going ship.

Gliding is done by riding the air column but turned at an angle or even horizontally. In short the aerodynamics of the bird is almost the same as that of a highly efficient monoplane.

One physiological condition in flight must be stressed. Although the sustained flight depends upon the strong breast muscles, yet they are reduced in the albatross, due to their habit of continuous soaring over the oceans riding the air currents, as a glider air craft does. On the other hand inspite of strong breast muscles, the fowl and the turkey are incapable of sustained flight. This is due to insufficient supply of blood to the flight muscles, as can be seen by the colour of the muscles (*white meat*) of the chicken and the turkey. Their flight muscles have few blood vessels (on account of low metabolism) and therefore appear white; while the *dark meat* of their legs indicates a good blood supply, on account of which they are efficient and tireless runners (high metabolism). Probably the fastest metabolising vertebrate on the earth is tiny humming bird, which shows the amazing hovering flight like a bee over a flower. While hovering it consumes about 80 cc of oxygen per gram of body weight per hour (other birds consuming hardly 20 cc's). Even at rest its metabolic rate is more than fifty times higher than man's.

MAMMALS

Locomotion in mammals

The subject of mammalian locomotion has not been thoroughly worked out so far. However, generally speaking, mammals have five distinct modes of locomotion on land, water and in the air: (1) walking, (2) running, (3) leaping, (4) swimming, and (5) flying.

The horse (the most cinematography) has four (3) canter, and (4) gallop.

(1) *Walking*.—Mammals have a quadrupedal mode of locomotion, which in case of man has become bipedal. In quadrupedal locomotion as "pushers" legs and knees forward. This centralises the long bones of the appendages under the body. The "push" of the hind legs is more effective in locomotion than the pull of fore legs.

Almost all primates can stand on their hind limbs and may occasionally walk in this. A complete walking cycle heel-strike of one leg to.

(2) *Runnings*—All fast and easily running mammals (cursorial) have evolved from good walkers; and speed and endurance are the characteristics of these cursorial mammals. A full cycle of motion is called a *stride*; and speed is the product of length of stride times rate of stride.

Longer legs take longer strides, and thus produce faster speed (horse, cheetah, impala, deer etc.) (Fig. 22). Natural selection has produced fast particular length of the body (foot, shank, hand and fore-arm) are elongated with respect to the segments close to the body (thigh and upper arm) as in the horse. In addition, the flexibility of the backbone in carnivores, speeds up the motion of its body, as well as of its legs.

Other modifications in cursorial mammals to increase speed, besides lengthening of the limbs, are:—

(1) The progressive change from plantigrade (man, apes)

to digitigrade (cats, dogs), and finally to unguligrade (one toe-horse; two toes-camel, antelope). Even the plantigrade man becomes unguligrade (runs on toes) when making a hundred yards dash.

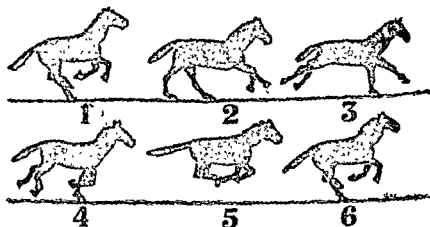


Fig. 22. Stages in one stride of the horse in full gallop.

- (1) First hind foot-fall.
- (2) Second hind foot-fall.
- (3) First front foot-fall.
- (4) Second front foot-fall.
- (5) Unsupported period.
- (6) First hind foot-fall.

(modified after Hildebrand)

- (2) The absence of coracoid and clavicle in hoofed mammals, and the reduction of clavicle to a vestige in carnivores, gives them freedom of movement of the shoulder blade in fast locomotion.
- (3) The shoulder blade pivots from a point about midway in its length, adding about $4\frac{1}{2}$ inches to the stride in large running mammals (cheetah, horse).
- (4) The suppleness of the back-bone increases the length of the stride by several inches, through lengthening of the back by extension, when the hind feet are pushing against the ground. The cheetah is the acme of this long-striding specialisation for speed, by back-flexing

and supplementing its wrist-flexing by slipping the shoulder blades up on the ribs about an inch. It thus achieves a smooth forward motion.

(5) Fast runners have increased their speed by increasing their length of stride (the horse and the cheetah both have a 23 feet stride) as also by the rapidity of successive strides (the cheetah has about 3.5 strides per second and the horse about 2.5).

(6) The important mechanism for speed, is the co-ordinated movement of as many joints as possible in the same direction at the same time. The shoulder blade and the pelvis are always rotating in the direction of the winging limbs. (The pelvis of man rotates considerably while walking and running, as shown by Muybridge, which is more marked in hip-swinging females than in males).

(3) Leaping.—The running jump practised by some animals is called leaping; the common examples of which are the Rabbit and Hare, the Deer and Antelope the horse and man etc. The leap is accomplished by sudden lengthening of the running stride by sudden extension of flexed limbs and backbone, with a sudden push of hind limbs. As in the frog, the thigh, shank and pes remain folded and flexed to form a low Z position. These are suddenly straightened out, with a backward kick of the hind limbs on the ground; and while running all the four limbs take part in this push. This drives the animal upward and forward in a leap.

In speedy runners and leapers (as in Deer) the body is compressed and the limb joints highly flexible, slender and tapering. Jumping locomotion of Kangaroos, Jerboos *etc.* are effected by the much longer hind limbs, feet and the tail, which all help in achieving the jump from a resting position. The Tiger takes a running leap on its prey and its *spring* is not a jump from the resting position.

(4) *Swimming* — Swimming mammals, such as the whales and porpoises and seals, do not paddle about the sea with their Oar-like flattened limbs, which are used chiefly for balance and up and down movements. The main propelling organ is the tail and caudal fin. The mechanism of tail movements for rapid locomotion has been studied in detail recently in the porpoise. The action is similar to the screw propeller of a ship, and not the side to side movement as seen in the fish tail. This is due to the horizontal position of the caudal fin in aquatic mammals (unlike that in fishes where it is vertical). Besides their bodies become spindle-shaped to cleave through the water.

(5) *Flying*.—Flying mammals, such as bats and flying foxes, have long delicate fore limbs and fingers, to support their thin membranous wings. The flying squirrels, lemurs, and Dermoptera have normal limbs with lateral extension of skin along the body and limbs (*patagium*), by which they *volplane* downwards from a height.

Chapter II

NUTRITION (DIGESTIVE SYSTEM)

All organisms, animals as well as plants require food for supply of energy and growth. The food requirements of plants are different from animals. Most plants use the energy of sunlight to change CO_2 from the atmosphere and water into sugar, the process being called Photosynthesis. Animals, on the other hand, generally consume solid food, consisting mainly of carbohydrates, proteins, fats and inorganic salts. Animals take in water separately, unlike plants.

There are four main types of nutrition according to the mode of feeding in the animals: holozoic; holophytic; saprozoic and saprophytic. In holozoic nutrition animals ingest solid organic food, which is digested and ultimately absorbed and incorporated in the tis nly in some simple ar : h possess photosyn- th Saprozoic and Sapro-phytic animals absorb dissolved organic compounds as food, as in many mastigophoran protozoa. Lastly, Parastic nutrition is characterised by absorption of ready-made organic food in solution (amino acids, sugars, dissolved fats and salts), from the host's body through general body surface or an alimentary system.

Physiologically, animal nutrition can be classified, according to the source of essential Carbon and Nitrogen requirements, into autotrophic and heterotrophic nutrition. Autotrophic organisms can synthesise all essential organic compounds from inorganic sources,

the C being obtained from CO_2 of air and N from the inorganic minerals. These include the chemotrophs (chemosynthetic bacteria) and Phototrophs (chlorophyll bearing organisms). However, there is another category called Mesotrophs, which can elaborate essential organic compounds from inorganic sources, but require holozoic or saprozoic feeding for certain vitamins and growth factors to synthesize the food. Heterotrophic nutrition is characteristic of almost all higher animals excepting parasites, and this process of nutrition entails ingestion, digestion, absorption and assimilation.

Nature of Foods.—The life processes of an animal require various complex foods. In the main the animal food is composed of five elements, C, H, O, N, S, and P. Besides, C, K, Na, Mg, Ca, and Fe are also essential. According to their natures the food substance are classified as under:—

- (1) Carbohydrates;
- (2) Proteins;
- (3) Fats;
- (4) Vitamins;
- (5) Inorganic salts; and
- (6) Water.

1. Carbohydrates — sugars
 Carbohydrates are the chief source of energy in most of the animals. These are simple sugars or compounds formed by the combination of simple sugars. Most of the carbohydrates have a formula in which the ratio of Carbon to Hydrogen to Oxygen is 1 : 2 : 1 i.e. CH_2O .

Carbohydrates are of three types: monosaccharides, disaccharides and polysaccharides. Monosaccharides are simple sugars which are crystalline and colourless having a sweet taste. The usual formula of a monosaccharide is $(\text{CH}_2\text{O})_n$. Monosaccharides are further divided according to the number of carbon atoms in a molecule. Those with the smallest number i.e. three, are called triose, those with four tetroses; with five pentoses and so on. Important examples

of monosaccharides are D-fructose (fruit sugar, and D-glucose (grape sugar or dextrose). These two sugars are readily absorbable by all animals, Disaccharides are formed by the condensation of two monosaccharides with the elimination of H_2O . Their general formula is $C_n(H_2O)_{n-1}$. Like monosaccharids these are also crystalline, easily soluble in water and sweet in taste. The important disaccha sucrose (cane large numbe- ing to their component units e.g. pentaosans $(C_5H_8O_4)_n$, hexosans $(C_6H_{10}O_5)_n$, and so on. They are usually tasteless and noncrystal- line and are not readily soluble in water. The important polysaccharids are cellulose, glycogen and starch.

2. Proteins

Proteins are universally present as cell constituents. They are remarkable for the large size of their molecules due to a high molecular weight. Molecular weight of water is 18; salt 58; glucose 180; while virus proteins molecular weights range from 10 to 8,500 millions. But the protein molecule is always made up of smaller building blocks called aminoacids. Aminoacids are colourless crystalline compounds which form salts with both acids and bases. Some important amino-acids are:—

I. Neutral Amino-acids

1. Glycine $HCH(NH_2).COOH$
2. Alanine $CH_3.CH(NH_2).COOH$

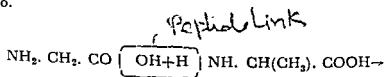
II. Acidic Amino-acids

1. Aspartic acid $HOOC.CH_2.CH(NH_2).COOH$
2. Glutamic acid $HOOC.CH_2.CH_2.CH_2(NH_2).COOH$

III. Basic Amino-acids

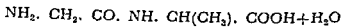
1. Arginine
 $NH=C(NH_2).NH.CH_2.CH_2.CH_2.CH(NH_2).COOH$
2. Lysine
 $CH_3.(NH_2).CH_2.CH_2.CH_2.CH(NH_2).COOH$

Proteins are synthesized in animal tissues from aminoacids, which again are synthesized by RNA, DNA action in the cell. There are several ways in which a protein may be synthesized. A method is squeezing an H-atom from the amino group of one aminoacid and an OH from another and then combining the two.



glycine

alanine



glycylalanine

This process of synthesis is called condensation, and a large number of such condensations combine to turn out some of the giant protein molecules found in flesh or muscles. The aminoacids join together ordinarily by successive coupling of amino and carboxyl groups, termed peptide linkage ($-\text{CO}-\text{NH}-$). If two aminoacids are joined by a peptide link ($-\text{CO}-\text{NH}-$) the compound is called dipeptide (e.g. glycylalanine); with more aminoacids we get tripeptides, tetra-peptides and polypeptides; depending upon the number of aminoacids. It should be noted that aminoacids are not arranged haphazardly but in a pattern common to all proteins. The arrangement may be spherical or helical.

3. Fats or lipids

All animal tissues contain some fats. Fats are insoluble in water but are soluble in organic solvents e. g. ether, benzene etc. Fats may be classified into; simple fats, compound fats and derived fats. Simple fats are esters of fatty acids with alcohols. Compound fats are esters of fatty acids with alcohols and other group; whereas the derived fats are derived from the above groups by hydrolysis. Examples of simple fats are butter, beef fat, olive oil and coconut oil, compound fats include lecithin, kephalin, plasmalogen (all

found abundantly in the brain). The derived fats include fatty acids and steroles.

Fatty acids are long chain compounds of general formula $R \cdot COOH$. These are of saturated fatty acids valer satisfied by single bonds; are held by double bonds. Common fatty acids are; formic acid, acetic acid, butyric acid etc.

Steroles include bile acids, vitamin D and the sex hormones. One of the best known steroles called cholesterol is abundently found in nervous tissues. It forms about 17% of the solids of human brain.

4. Vitamins

Vitamins have often been termed accessory food stuffs but they are in reality essential food stuffs without which no animal can live for long. At first they were considered to be amines, thus the name vitamin (vital amines). Vitamins are required only in small quantities and all vitamins are essential for all animals since some can be synthesized by the body of some animals. For example vitamin C which prevents scurvy is an essential dietary requirement for man, monkeys and rodents, but all other mammals seem able to synthesize it. Similarly vitamin K, which is necessary for blood coagulation is synthesized by all mammals by intestinal bacteria (intestinal flora). Vitamins are of two kinds:—(1) water soluble; (2) fat soluble. The water

The fat soluble vitamins are A, D, E and K.

The formula, food sources, functions, and diseases in man caused by deficiency of each one of these vitamins is given in the table:—

ANIMAL-PHYSIOLOGY

VITAMINS

Name, formula, solubility	Sources	Function	Deficiency result
A ($C_{20}H_{30}O$) fat soluble	Green leaves, Carrots Cod or shark-liver oil, egg-yolk and milk	Regeneration of rhodopsin	Dry Cornea, night blindness in man.
B_1 (Thiamine) $C_{12}H_{17}N_4OSCl$ water soluble	Brewer's yeast, un- polished cereals, and liver	Needed for Carbo- hydrate metabolism	Loss of appetite; Beriberi in man.
B_2 (Riboflavin) $C_{17}H_{19}N_4O_6$ water soluble	Green leaves, milk egg-white, liver, meat, yeast	Essential for growth	Inflammation of cornea and crackings and soreness at the corners of mouth (Cheilosis) in man.
B_3 (Pyridoxine) $C_8H_{11}NO_3HCl$ water soluble	Yeast, whole cereals, milk, liver	Needed for amino- acid metabolism	No deficiency disease indenti- fied man. Anamia in dogs; Dermatitis in rats.
B_{12} (Cyanocobal- min) ($C_{64}H_{88}N_{14}O_{14}$) $PClO_4$ water- soluble	Fish, liver, meat milk, egg-yolk	Needed for amino- acid metabolism	Perniciousanaemia in man.

Name, formula, solubility	Sources	Function	Deficiency result
C ₆ (Ascorbic acid) (C ₆ H ₈ O ₆) water soluble	Citrus fruits, tomatoes, Animals produce Vitamin C (except primates and guinea pigs).	Needed for the formation of inter-cellular cement and maintains the integrity of capillaries.	Bleeding gums, loosened teeth (Scurvy) in man.
D ₂ (Calciferol) (C ₂₈ H ₄₄ O) fat soluble	Fish liver oils, eggs, formed by exposure of skin to ultraviolet light.	Needed in Calcium and Phosphorous metabolism, for normal growth and bone development.	Softening of bones and consequent deformities (Rickets) in young.
E ₁ (Tocopherol) (C ₅₆ H ₁₀₀ O ₂) fat soluble	Green leaves and vegetable fats.	Antisterility vitamin, necessary for normal reproduction.	Sterility in rats, mice and poultry. Weakness and degeneration of skeletal muscles in young animals.
H ₁ (Biotin) (C ₁₀ H ₁₆ N ₂ O ₃ S) water soluble	Liver, Kidney, Eggs, and yeast, produced by the intestinal bacteria in man.	Essential for growth in birds.	Dermatitis in rats porosis in birds.

Name, formula, solubility	Sources	Function	Deficiency result
K, ($C_{31}H_{48}O_2$) fat soluble	Green leafy vegetables; manufactured by intestinal flora in man.	Essential for the formation of Prothrombin.	Haemorrhage
M, (Folic acid) ($C_{14}H_{16}N_2O_6$) water soluble	Green leaves, soyabean, yeast, egg-yolk.	Essential for growth, and formation of blood cells.	Anaemia
P, (Criticin).	Lemon Juice	Prevents fragility of capillary walls in conjunction with Vitamin C.	Bleeding due to breakdown of capillaries.
P. P. (Niacin) ($C_6H_5NO_2$) water soluble	Brewer's yeast, wheat, gram, rice husks, milk, green vegetables.	Essential for cellular function, as constituent of certain co-enzyme.	Roughened skin, sore mouth, pink tongue, Nervous disorder (Pellagra); in man.
Pantothenic acid ($C_8H_{17}NO_5$) water soluble.	Yeast, yolk, milk, liver, and a host of other human foods.	Forms Coenzyme 'A'	Dermatitis in chicks; Graying of fur in black rats, Nerve degeneration in pigs.

5. Inorganic Salts and Trace Elements

Mineral salts are an essential constituent of the food requirement in animals. They are essential not only for normal development of bones, teeth, muscles, nerves, heart and blood etc, but are indispensable as ions for the vital phenomenon of osmoregulation. The important inorganic salts required for nutrition are: sodium, potassium, magnesium, calcium, iron, sulphur, phosphate and iodine. The Trace elements required by animals are; chromium, copper, manganese, molybdenum, zinc, cobalt and vanadium.

Sodium, normally ingested as common salt by man, is also present in small amounts in milk, vegetables, and meat. Sodium and potassium chlorides and bicarbonates regulate osmotic pressure; deficiency of sodium causes painful cramps in muscles, which can be cured by drinking saline water. Potassium helps in regulating normal growth and normal functioning of muscles and along with sodium is responsible for osmoregulation. However, excess of potassium is harmful for the heart, which may stop beating. Magnesium is again essential for ionic balance and for development of bones, muscles and nerves. It is an activator of enzymes. Its deficiency causes retarded growth, nervous disorder and irregular ome

growth of bones, teeth, muscles, nerves etc, and is for
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calcium, as it has an essential role in the formation of respiratory pigment, haemoglobin. It acts as a catalyst in many enzymatic reactions. Its deficiency causes failure of R. B. C. and haemoglobin production in blood and finally respiratory failure. Sulphur is necessary for synthesis of body proteins. Its deficiency has been seen to retard normal growth. Phosphate is the chief source of phosphorous, which is essential for the formation of bones, muscles and blood. The ATP-ADP reactions, so necessary in enzymatic and metabolic activities in the body are impossible without phosphorus. Its deficiency not only retards metabolism and growth,

but also causes poor development of bones and teeth. Iodine is responsible for the regulation of basal metabolic rate (BMR) of all animals. Iodine is essential for the production of thyroxine by thyroid gland. Its deficiency causes exophthalmic goitre in man, which can be cured by adequate doses of iodine.

Chromium forms a part of the permanent structure of R. B. C's. Copper is a constituent of haemocyanin in most arthropod and molluscan blood and also a part of some vertebrate enzyme. Manganese activates most oxidation processes in the body, as also actions of intestinal aminopeptidase and bone-phosphatase. Deficiency of manganese causes malformation of skeleton. Molybdenum occurs in some enzymes including xanthine oxidase, which is important in the formation of uric acid. Zinc is a constituent of carbonic anhydrase and other respiratory enzymes. Cobalt is an essential component of vitamin B₁₂ and thus necessary for formation of blood cells and growth, specially in cattle which require it more than other animals. Vanadium is present in the respiratory pigment of marine animals, specially ascidians.

6. Water

Water is taken in by most animals in large quantities and forms the major constituent by weight, of every animal, where there is no water (as on the moon) there can be no life. Its uses in the body are numerous: (1) it is an unsurpassed solvent, (2) it brings ions, and atoms; (3) it (4) for osmoregulation circulation; (5) its vital role in the cell. The phrase 'no water no life, either plant or animal' aptly stresses the importance of water.

Feeding Mechanisms

There are various methods by which an animal obtains its food, depending upon the animal group to which it belongs, and more so on the nature of the food. Broadly speaking animals can be divided according to feeding mechanisms into four types

(Polychaeta); *Octopus Sepia*, *Loligo* (Mollusca); and sea-cucumber (Echinodermata).

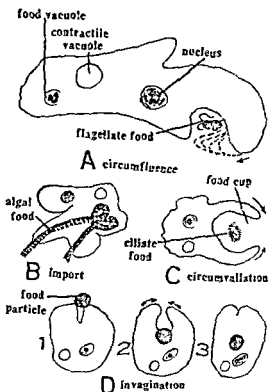


Fig. 23. Four types of food ingestion in *Amoeba*.

— There are some peculiar macrophagus feeders. Almost all coelenterates have special stinging cells, (*Nematocysts*) by which the food prey is paralysed (hypnotoxin) before ingestion. Poison is also injected by the larva of *Dytiscus* (Coleoptera), spiders and scorpions (Arachnids) most cephalopods (Mollusca); and poisonous lizards and snakes (Reptilia) for capture of food prey. Peculiar is the electrocution of prey by electric fishes (*Torpedo* and *Electric Eel*). Still more peculiar is the feeding habit of the star fish, which extrudes its stomach over its bivalve prey after opening the shell by its numerous tube feet. Similarly, external digestion (before ingestion) is found in bowfly larvae and in the scorpion.

Detritus Feeders.—Detritus feeders feed on organic matter in soil and mud by the protruded pharynx; but others like the Holothurians shovel sand into the mouth. A few fishes, such as the sturgeon (*Acipenser*) and the carp (*Cyprinus*) feed habitually on bottom detritus of streams and lakes. In all these cases the detritus ingested contains a large amount of organic particles, which is used as food, the rest consisting of mineral matter being passed out unchanged through the body.

Fluid Feeders.—Animals feeding on liquid food are common, such are the sap-sucker butterflies and moths; sponging and lapping bees and blow flies; the mosquitoes and sand flies; bugs and lice; ticks and fleas; all of which have different types of sucking or

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Parasitic feeding, apart from fluid feeding is by osmosis and is characteristic of all extreme endoparasites, such as the Sporozoa (protozoa), Cestoda (platyhelminthes) and Rhizocephala (crustacea).

Symbiotic feeding.—Symbiotic feeding may be classified apart from the other types of feeding mentioned above. In this two animals depend on each other for their food and feeding, e. g., the hermit crab places a sea-anemone on its back and then proceeds to feed on particles dropped by it. Similarly wood-feeding roaches and termites have symbiotic humbugs.

proteins.

Digestion

Digestion in animals begins after the ingestion of food. It is of two main types: (1) intra-cellular digestion; (2) extra-cellular digestion. Intracellular digestion is found in protozoa, sponges, some coelenterates and in the phagocytes (WB. CS) of the blood of

higher animals. It is the most primitive way of feeding in which the food particles are taken inside a cell, in a food vacuole for

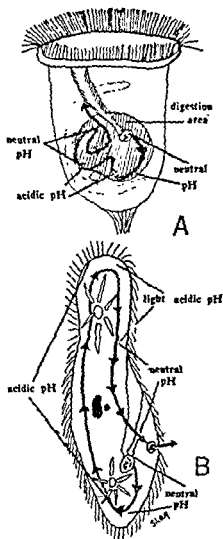


Fig. 24. A—Cyclosis in *Carchesium*.
(After Green wood)
B—Cyclosis in *Paramecium*.
(After Shapiro)
(Note—areas of Neutral and acid digestion).

digestion, (Fig. 24). The development of a digestive tract (enteron)

is seen first in the simple coelenterate, **Hydra** ; but even here, there is a certain amount of intra-cellular digestion by the pseudopodia bearing cells lining the coelenteron.

Extra-cellular digestion may also be of two types : (1) external ; (2) internal digestion. External digestion is seen among some macrophagus feeders, such as the ciliate **Glaucoma** which produces an external proteinase. Amongst invertebrates the star fishes extrude the stomach over the prey, and a considerable amount of digestion takes place before the food is ingested. Most cephalopods and spiders inject a protease enzyme into the living prey, the external digestion being so complete that only liquid food is taken into the body of the feeder.

Mechanical break down of food.—In internal digestion mechanical maceration and trituration usually precedes digestion. In crustacea the food is torn by the chelae, the food being held in the mandibles. Other crustacea as well as earthworms have a gizzard with hard internal chitinous teeth to macerate the food ; insect jaws and palps are used for the same purpose. The radula of gastropods is used for rasping vegetable matter. The muscular

Dasypeltis, in which the haemal spines of the cervical vertebrae project into the oesophagus and break the egg shell as it passes down.

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Physiology of Digestion

Enzymes.—Digestion is by chemical reactions of organic compounds at an extremely high rate, through the agency of certain biological catalysts called enzymes. All enzymes are proteins which

are specific, heat susceptible, organic catalysts manufactured by living cells, acting independently of them. The majority of chemical reactions occurring in an animal are enzymatic in nature e.g., digestion, cellular respiration, muscular contraction and a host of other processes.

An enzyme which brings about hydrolysis is called hydrolase. Hydrolysis is the splitting of a substrate (substance on which the enzyme acts) by the addition of water. Almost all digestive enzymes are hydrolases, but due to their action they are classified according to substrates which they hydrolyse:—

- (1) Carbohydrates: which split the higher carbohydrates into simpler ones and finally into absorbable simple sugars;
- (2) Proteases: which split the peptide linkage of complex proteins and convert them in stages as proteases, peptones, peptides and finally into aminoacids;
- (3) Esterases: which attack the ester linkage of esters and hydrolyse them;
- (4) Nucleases: which hydrolyse nucleic acids.

Besides being susceptible to temperature, pH and the presence and absence of other enzymes, a peculiarity of all enzymes is that they need to be activated in some manner e.g., the precursor of pepsin in zymogen present in the secreting cells of stomach, which is activated by a hormone Gastrin. The main hormones regulating secretion of digestive enzymes are (Fig. 81):—

- (1) gastrin, activates zymogen, producing pepsin as well as secretin of Hel;
- (2) entrogastriene, inhibits acid secretin by the stomach and is thus antagonistic to gastrin;
- (3) cholecystokinin: brings about the contraction of gall bladder releasing bile in the intestine;
- (4) secretin, activates the secretions of liver and pancreas;
- (5) pancreozymin, stimulates the secretion of pancreatic enzymes;

resistent to vertebrate digestion (for example, a wooly ball is formed in the stomach of cattle, collected by licking their skins that can be digested). Cellulose is digested by many invertebrates,

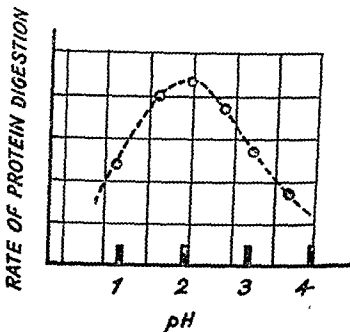


Fig. 25. *Rate of protein digestion in the intestine of the earthworm.*
(After Mueson)

such as roaches, termites and even cattle to some extent. This is done by a special enzyme called *cellulase* or *cellulobiase* secreted by their intestine or by microbes converting cellulose into sugar.

Protozoa digest their food in food-vacuoles, which undergo *cyclosis* in the cell and become rapidly acid, *e.g.*, the vacuolar contents may have a pH of 4 in *paramecium*. After digestion the acid concentration in the food vacuole returns to *neutral i. e.* to pH 7. In general, protozoa digest proteins easily, while they have difficulty with carbohydrates and fats. However, *Ameoba proteus* digests fats to fatty acids and glycerol; but *A. dubia* takes some days to digest injected oils.

fine particles or solutions can pass through. Surprisingly they also have bile salts similar to that of vertebrates, to help in the digestion of fats; while some decapods and copepods have peritrophic membrane similar so that of insects.

Some ectoparasitic insects (mosquitoes and blood sucking flies) also secrete an anti-coagulant to prevent the clotting of blood. In most insects the labial glands contain a digestive enzymes, *e. g.*, amylase in cockroach, protease in larval diptera *etc.* The food is stored in the crop, which has no digestive secretions, but some digestion may take place here by enzymes of labial glands, already mixed with the food or by the enzymes of the mid-gut being passed forward into the crop. Although most of the digestion in insects is in the mid-gut, in the cockroach fat is digested by yeasts and bacteria in the crop. Insects have a peculiar saccular digestion, in the mid-gut. The food on leaving the fore-gut is enclosed in a thin, chitinous sac called the *peritrophic membrane* which is permeable to both enzymes and digested food. Such a peritrophic membrane is absent from fluid feeding insects *e. g.*, butterflies, moths, bugs, fleas and lice. The chief function of the hind-gut in insects as well as in most of the invertebrates is to absorb water, loss of which may lead to dessication and death. It is amazing that many adult butterflies have no digestive enzymes at all except for invertase, since they feed on sugary solutions.

The *molluscs* are peculiar in having most of their digestion as intra-cellular, although proteolytic and lipolytic enzymes are liberated into the gut by breakdown of digestive diverticulae (Fig 26). In the gut of some mollusca is present a *crystalline style*, made up of *globulin* (a protein) which contains the enzyme amylase. This peculiar crystalline style is secreted in the style sac in the intestine and is rotated forward by means of cilia. It is gradually worn down in front to liberate the amylase. In many molluscs there is a special filtering mechanism which allows only small particles to pass into the digestive diverticula, where further intra-cellular digestion takes place.

In *echinoderms* digestion is extra-cellular in the main, although final digestion is intra-cellular, within the stomach and pyloric caeca cells. The cardiac stomach secretes only mucus, while it is

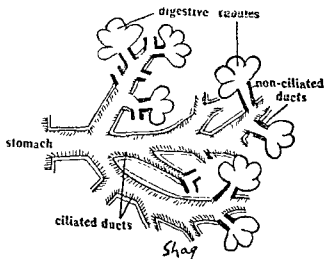


Fig. 26. Arrangement of Digestive ducts and tubules in the digestive gland of an Eulamellibranch.
(After Owen).

the pyloric caeca which secrete the digestive enzymes—protease, amylase and lipase. As already stated digestion before ingestion is characteristic of the star-fishes, the enzymes being poured outside its own body into the body of the prey, after which the partly digested semi-fluid food is taken in, when the stomach is retracted.

Digestion in vertebrates (Fig. 27)

The general process of digestion in all vertebrates is rather similar and follows almost the same pattern as in mammals. However salivary digestion is rare in fishes, amphibia, reptilia and most birds. Surprisingly, an amylase has been demonstrated in the buccal secretion of frogs and toads and also in the fowl. In bony fishes no amylase is present in buccal secretion, amylase and maltase being secreted predominantly by the pancreas.

The stomach in the lower vertebrates secretes a pepsin-like enzyme which is activated in only acid medium. Proteases are

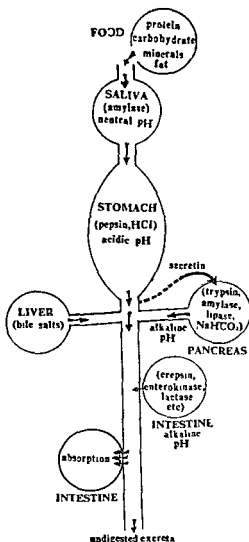


Fig. 27. Diagrammatic representation of Digestion in vertebrates.

secreted in the intestine in the main, while amylase, disaccharase and lipase are also secreted by the intestine (Fig. 27). In some fishes and birds small amounts of gastric lipase has been found.

Although all these enzymes are very similar in their chemical composition in the classes of vertebrates, individual specificity of the enzyme has been shown in fish pepsin, which is different from the pepsin of birds and mammals. Similarly proteases of the fish amphibia, reptiles and mammals are specifically different.

The acid pH of the stomach contents is not so high in fishes, amphibia and birds, as in the mammals, being only about 4 to 4.5. In some fishes such as rays, and some bony-fishes the stomach is surprisingly alkaline, although pepsin is present. However, the carnivorous sharks have a stomach acidity twice that of man. In such fishes where a stomach is absent as in Holocephali and in herbivorous teleosts, little pepsin is demonstrable. This absence of stomach may be primary or secondary. In primitive fishes, such as Cyclostomes, a stomach has not developed at all. The herbivorous bony fishes, such as carps, have lost the stomach secondarily, due to vegetable low protein diet, in contrast to sharks and carnivorous fishes which have a high protein animal diet for digestion. That originally the stomach was developed in vertebrates as a food storage organ, is demonstrated by the fact that **more pepsin is produced by the oesophagus than by the stomach, in frog.** In birds there is some digestion in the crop, mainly by autolysis and by bacteria.

Digestion in Mammals (Digestive Juices)

The digestive glands in mammals are :

(1) salivary glands, secreting *saliva* ; (2) gastric glands, secreting *gastric juice* ; (3) pancreas, secreting *pancreatic juice* ; (4) liver secreting *bile* ; and (5) intestine, secreting *succus entericus* or intestinal juice.

1. Salivary juice

The salivary glands in mammals are usually three pairs; parotids; submaxillaries and sublinguals. Parotids secrete the enzyme ptyalin; the sublinguals secrete only mucin; while the submaxillaries secrete both ptyalin and mucin.

Ordinarily some saliva is secreted to keep the mouth continuously moist; but with the stimulation by sight, smell or taste of food, the secretory rate is increased more than tenfold. The stimulation is effected by a nervous mechanism, the salivary glands being innervated both by sympathetic and parasympathetic nerves, fibres of which are present in both the 7th and 9th cranial nerves supplying the salivary glands. These fibres arise in a region of the medulla oblongata called salivary centre, which receives nerve impulse from higher centres of the brain. There is thus a salivary reflex caused by sight, smell or taste of food, (The dryness of the mouth in an embarrassed speaker is due to inhibition of the salivary centre in medulla, from the higher centres located in cerebral hemispheres).

The digestive function of saliva is due to the salivary amylase called ptyalin which acts on starch. Starch is hydrolysed as follows:—

Starch + Amylase \longrightarrow Erythro-dextrin + maltose \longrightarrow Achroo-dextrin maltose \longrightarrow Maltose (the absorbable end product of carbohydrates). The main site of salivary digestion is the stomach and not the mouth, since food remains only for a very short time in the mouth.

The functions of saliva are as follows:—

- (1) It moistens and lubricates the food, and helps in forming food bolus and deglutition;
- (2) It digests starch and glycogen;
- (3) It dissolves food substances and renders them fit for tasting (undissolved food cannot be tasted);
- (4) It has a role in water regulation of the body;

- (5) It has cleansing action on mouth and teeth; and
- (6) It serves as a route for excretion of some amounts of urea and uric acid.

Certain odoriferous substances are secreted through saliva into the mouth from the blood. If onions are placed directly in the stomach without chewing, within a few minutes these can be smelt in the mouth. The allyl sulphide of the onion is absorbed in the blood and then excreted with the saliva.

2. Gastric juice

Gastric juice is a clear, colourless, sour, acid, watery fluid (usually pH 1 to 3). It consists of 99% water and 1% HCl, enzymes, inorganic salts and an intrinsic factor which acts on an extrinsic factor in food to form an *anti-anemic principle* (lack of these factors lead to anemia). The stomach lining in man has about 35 million gastric glands, which are usually branched in cardiac stomach and coiled in the pyloric stomach. There are three types of gland cells in the stomach: (1) mucin cells or goblet cells secreting mucus;
(2) enzyming HCl.

There are three phases in gastric secretion:—

(1) The *cephalic phase*, when the sight, smell or taste of food causes, secretion of *appetite juice* by reflex action, controlled by the vagus nerve. Vagal stimulation results in the production of highly acid juice rich in pepsin.

(2) The *gastric phase*; which is elicited by the passage of food into the stomach and is due to the chemical stimulation of the gastric glands by a hormone called *gastrin*, produced by the gastric mucosa.

(3) The *intestinal phase*; when there is gastric secretion due to a hormone *secretin* from the duodenum, and is the last phase of gastric secretion.

The important enzymes in gastric juice are pepsin, rennin and small amounts of lipase; the HCl concentration being about 0.5 percent. Pepsin is a powerful protease splitting proteins into protoes and peptones, only small amounts of amino acids being formed. Rennin acts on the caseinogen of the milk and yields paracasein, which combines with calcium to form curdy calcium paracasein. This is then attacked by pepsin. The lipase activity of gastric juice is a slight hydrolysis of fats.

The functions of HCl in the gastric juice are many :—

- (1) It provides a suitable acid pH for action of pepsin;
- (2) It activates pepsinogen which is converted into pepsin;
- (3) It hydrolyses some sugars and fats,
- (4) It acts on prosecretin to convert it to secretin which activates gastric, pancreatic and bile secretions;
- (5) It is bacteriocidal in action;
- (6) It can hydrolyse certain forms of cellulose to some extent; and
- (7) It plays an important role in cardiac and pyloric sphincter control.

3. Pancreatic Juice

The food is churned in the stomach by the action of powerful gastric muscles and mixed with the salivary and gastric juices. This partly digested food forms an acid chyme which is passed into intestine and converted into more fluid chyle. Further digestion now takes place by the action of pancreatic juice, bile juice and intestinal juices.

Pancreatic juice is a colourless, alkaline, watery fluid containing enzymes and inorganic salts. The chief enzymes are :—

- (1) amyllopsin (amylase);
- (2) sucrase;

- (3) *trypsin* (protease);
- (4) *polynucleo-peptidase*;
- (5) *carboxy-peptidase*;
- (6) *protaminase*; and
- (7) *steapsin* (lipase).

Amylase acts on starches and dextrins to convert them into maltose. Sucrase splits sucrose (cane-sugar) into fructose and glucose.

Trypsin is formed from the precursor trypsinogen, which is activated by the intestinal hormone, enterokinase. Trypsin is a

polypeptides, and converts them into simple peptides and amino acids. On the other hand, polynucleopeptidase is a nuclease, which splits the nucleic acid molecules into nucleotides; while protaminase

mechanism, in which acid chyme extracts secretin from the mucosa of the duodenum. The hormone secretin is absorbed by the intestine. It enters the bloodstream and is imm

4. Bile Juice

Bile is a bitter, digestive juice produced by the liver. It enters the small intestine during the periods of digestion, when it is discharged by the bile reservoir

glycocholate, manufactured by the liver cells. The important physiological processes of fat digestion and fat absorption are due to the presence of bile salts. Strangely these salts are not only secreted into the gut but also undergo circulation with blood in the body and are in part reabsorbed and passed with portal blood into the liver, where they accelerate secretion of bile. They are finally excreted with the faeces. The bile pigments are *bilirubin* and *biliverdin*. Bilirubin is formed by the breakdown of haemoglobin, while biliverdin is formed by the oxidation of bilirubin. Finally these pigments are reduced by intestinal bacteria (specially in large intestine) into *stereo-bilogen* and *uro-bilogen*, which impart the characteristic colour to the faeces.

The main functions of bile are :—

(1) It helps absorption of fats by forming complex salts of fatty acids with bile salts; (2) it aids in emulsification of fats by bile salts, which lower the surface tension of large fat globules, which are broken up into smaller globules; (3) it serves as a channel for excretion of bile pigments, cholesterol, inorganic salts, toxins *etc*; (4) bile being alkaline, neutralizes the acid of the gastric juice; (5) bile salts are absolutely essential for absorption of vitamin K and all the fat soluble vitamins; (6) bile stimulates peristalsis and has a laxative effect (therefore doctors prescribe bicholates as laxatives); (7) bile helps in the liberation of secretin from the intestinal mucosa; and (8) bile precipitates proteases and retards their passage through the intestine, giving more time for digestion by the intestinal juices.

5. Intestinal Juice

Intestinal juice or *succus entericus* is secreted by the glands of Brunner and crypts of Lieberkuhn. The glands of Brunner secrete a proteolytic enzyme, which by HCl. On the other hand, the crypts of Lieberkuhn secrete an alkaline yellowish liquid, containing a large number of enzymes, hormones, inorganic salts and mucus.

The main enzymes in the intestinal juice (Fig. 27) are :—

- (1) erepsin—consists of aminopeptidase, acting on polypeptides, and dipeptidase acting on dipeptides, splitting them into amino-acids ;
- (2) enterokinase—activates pancreatic trypsinogen to produce trypsin ;
- (3) lactase, maltase and sucrase—act upon the polysaccharides
- (4) lipase—converts fats into fatty acids ; and
- (5) amylase—converts residual starch into sugar.

The main stimulus for the production of intestinal juice is the mechanical stimulus of the passage of chyle into the small intestine. However, the secretion is regulated both by chemical and nervous control. Of the hormones, enterokinin (a substance isolated from the intestinal mucosa) is a specific secretory hormone increasing the amount and enzyme content of the intestinal juice.

Digestive Enzymes

<i>Class</i>	<i>Enzyme/Source</i>	<i>Optimum pH</i>
Protease	Pepsin	2.0
	Trypsin	8.0
	Erepsin	7.7
Amylase	Ptyalin	6.9
	Pancreatic Juice	7.0
Lipase	Pancreatic Juice	8.0
	Gastric Juice	6.0

Some Peculiar Features of Digestion

1. Protection Against Self Digestion (Auto-digestion)

It is often asked why the strong proteolytic enzymes in the stomach and intestine of vertebrates do not digest the cell lining

of the alimentary canal. If pieces of stomach, intestinal wall *etc.* are kept in acid pepsin, they get rapidly digested. Yet the living stomach, intestinal wall and pancreatic cells remain intact for years, while producing enough pepsin, trypsin and other digestive enzymes, which would digest the whole animal, many times over. Why then is there no auto-digestion? The answer was unsatisfactory for many centuries. The main causes for prevention of auto-digestion are :—

(i) The proteolytic enzymes (pepsin and trypsin) are not elaborated as such in the stomach and pancreas glands cells. Instead, these cells secrete inactive molecules of pepsinogen and trypsinogen which are precursors of pepsin and trypsin respectively. When these inactive molecules reach the acid stomach or the alkaline intestine, they lose a few amino-acids from their enzyme molecules. This loss uncovers the active surface of the enzyme molecule, so that it can start the work of catalysis. Therefore the enzymes do not digest their own secreting cells.

(ii) The mucous cells that line the digestive tract secrete a layer of mucus which forms an effective barrier against the digestive enzymes.

(iii) It has been shown recently that the living cells of the gut secrete certain specific *anti-enzymes* which form a protective layer over the gut cells, counter-acting the action of enzymes.

(If pathologists require a piece of the stomach, intestine or pancreas for investigations, the material has to be collected within twenty minutes of the death of the man or the animal. After this period auto-digestion sets in and the cells form a digested mass).

2. Gut Ulcers

Ulcers are becoming increasingly common in most countries of the world. Recent estimates being 5% in Western countries and 10-20% in Kashmir and South India. *Peptic ulcer* is the erosion in the lining of any part of the digestive tract, as a result of auto-digestion by the action of the enzyme pepsin. This in

turn, is caused by an increase in acid content of gastric juice (hyperacidity) which activates pepsin digestion of mucosa. If HCl is introduced by continuous drip method into the stomach of a dog, ulcers invariably develop.

Surprisingly, besides unwholesome food, hyperacidity results from stress and strain of man in modern civilization. That, hyperacidity is caused by emotional stress, high strung nature and worry has been conclusively shown by *Wolf and Wolff* in U. S. A. Peptic ulcers are of two types:—(1) Gastric; (2) Duodenal

(1) Gastric Ulcer

Gastric ulcer is caused by excess of the hormone *Gastrin* secreted during the gastric phase of digestion. Due to this the gastric glands work, so to say, over time causing excess acid and pepsin to be secreted in the stomach. These secretions finally erode the stomach lining and may actually perforate the stomach wall in chronic cases.

(2) Duodenal Ulcer

It is the commonest ulcer in man caused by hyperacidity as also overwork by the duodenal glands. Duodenal ulcer can be differentiated from gastric ulcer, by the fact that duodenal pain starts after 3-4 hours of a meal, whereas the gastric pain starts with in the first hour of the meal.

Gut ulcers are dangerous as the man passes blood with faeces (*Black motion*) when the gut wall has been seriously corroded. In order to neutralize the hyperacidity in patients of gut ulcers antacids are prescribed (e.g. Aluminium hydroxide). In several cases *vagotomy* (removal of vagus which stimulates gastric glands) or even *gastrectomy* (removal of stomach) is carried out. A modern method is to lower the temperature of stomach. An inflatable balloon of the shape and size of stomach is inserted into the stomach of patient, into which ice cold water from a refrigerator is pumped. This cools down the rate of chemical activity of gastric glands. Stomach ulcers are cured in 80% cases if such stomach cooling is repeated several times.

Absorption

Nutrients absorbed are: (1) end-products of digestion, *viz.* glucose, fructose, amino acids and fatty acids; (2) inorganic ions;

(3) vitamins and (4) water. The main site of absorption is the intestine. However, amounts of some substances are absorbed in the stomach, such as alcohol, condiments and some drugs. Besides absorption of carbohydrate, fermentation occurs in the stomach of ruminant mammals, in which the stored food in the rumen (first chamber of the stomach) is regurgitated and ruminated (chewing the cud Fig. 28). This process enables salivary

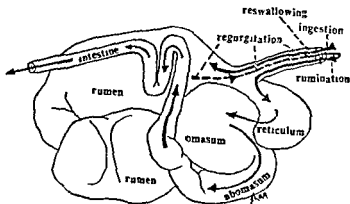


Fig. 28. Four stomach Chambers Ruminant (Goat, Sheep, Cattle)
Arrows indicate the course of food.

juice to mix thoroughly with the finely ground food during rumination. When the food enters the reticulum after reswallowing, it is mixed with gastric juice and only, then passed into the omasum and abomasum, where digestion take place. In other herbivores products of carbohydrate fermentation are absorbed partly in the caecum, but mainly in the colon.

The entire intestine is provided with thousands of villi which increase greatly the absorptive surface (Fig. 29). For example, the villi of the small intestine in man provided an absorption suface of about 10 Sq. meters, which is about 600 times greater than the internal area of a cylinder of the same dimensions. Absorption is not a matter of simple diffusion through the cell membranes of the intestinal mucosa; but it is selective. The

... .. 100% of fats as fatty

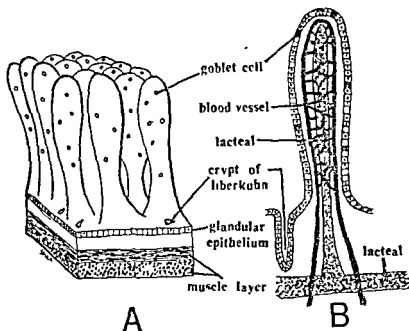


Fig. 29. A—Magnified view of mucosa of small intestine showing densely packed villi
B—A single villus—absorbing unit of small intestine, in L. S.

Absorption of Glucose. Glucose is absorbed even from hypotonic solutions. The rate of absorption of glucose (fructose, galactose and mannose) is twice as high as that of pentoses, when imbibed in equal concentrations. The capacity for selective absorption of sugars (Fig. 30) can be experimentally abolished by freezing the epithelial layer of the villi, when the rate of absorption of the different sugars becomes the same. It is evident therefore, that selective absorption requires a certain metabolic activity on the part of mucosa cells.

The absorption of glucose also involves the expenditure of energy. It is now believed that glucose becomes phosphorylated with phosphates made available by the breakdown of Adenosine Triphosphate (ATP) into Adenosine diphosphate (ADP). The intestinal mucosa has copious phosphatases, which appear to catalyse this reaction. Phosphorylation causes the maintenance of a

gradient for sugars between the gut lumen and the cells, the energy supplied by ATP being used for active transport, by moving molecules across cell membranes at a fast rate. (This is in contrast to non-active transport in the filtration of plasma through the renal glomeruli)

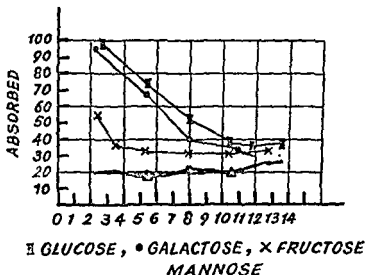


Fig. 30. Percentage absorption per hour of different sugars in the small intestine of rats. (After Verzar and McDougall).

Absorption of Proteins and Amino-acids

Rapid absorption, of amino-acids and other protein by-products is done by special concentrated patches of villi in intestine, called Peyer's patches.

The absorption of large protein molecules by young mammals at birth is a mechanism by which immunity is conferred on the young by absorption of antibodies in the colostrum of the mother (in ruminants, horses, pigs, and rats).

The rate of protein absorption can be calculated from the amount of amino-nitrogen in blood; as it increases correspondingly after a protein meal (Fig. 31).

Absorption of Fats. Fatty acids, the end products of fats cannot be readily absorbed unless there is presence of bile salts, which form easily diffusible compounds with them. Within the cells of the intestinal epithelium the absorbed fatty acids are

resynthesized into fat globules, which join the lymph stream of the

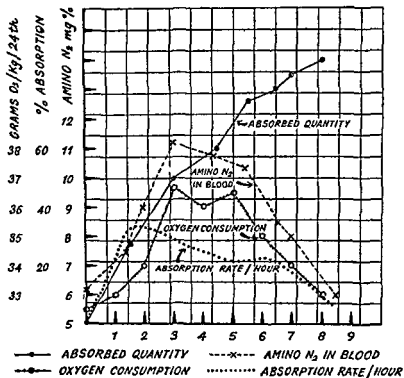


Fig 31. Absorption of Raw meat by rats (After Verzar and Mc Dougall).

thoracic duct or fall into the portal blood stream. Phospholipids and cholesterol are absorbed without any change.

Absorption of Inorganic Ions. Ions pass through the gut wall against concentration gradients (selective absorption). NaCl is absorbed as quickly as dextrose; other chlorides and acetates are absorbed more quickly than lactates and nitrates; sulphates and phosphates are absorbed at a very slow rate. The phosphates pass through the gut wall as phospholipids. Iron is only absorbed as an ion as a component of any other organic substance. When iron falls short the result is anaemia. Absorption of calcium is effected by the pH of the intestine. It is only absorbed in a water soluble form and if not precipitated in the intestine by any other constituent of the diet. Amino acids and bile promote its absorption and so does Vitamin D.

Basal Metabolic Rates

The basal metabolic rate (BMR) of different animals is determined by the amount of oxygen used per gram of body weight per hour. These are given in detail in the Chapter on Respiration.

Temperature Regulation and Heat Balance

All living organisms have a narrow range of temperature tolerance, ranging from -1°C to $+50^{\circ}\text{C}$ and a body temperature from 2°C to about 38°C . All poikilotherms (cold blooded animals) change their body temperature according to their surroundings, *e. g.* an earthworm has the temperature of the soil in which it lives; the fish the temperature of water in which it swims; and the frog, water temperature when aquatic and air temperature when on land. Homoeotherms (warm blooded animals) on the other hand have to regulate their body temperature and hence have a budget of heat balance. Such animals are confined to the birds and mammals.

Poikilotherms

In poikilotherms, insects and reptiles of deserts cannot withstand the high desert temperatures of above 50°C even for a few minutes. They survive in their natural habitat by escaping from the heat by burrowing, going into shade or water. There is however some heat balance by heat loss through conduction, convection and evaporation; and this is somewhat balanced against the heat gained through radiation of the sun and metabolism of the body. Insects as a whole can withstand far higher and lower temperatures than other poikilotherms, *e. g.* some springtails and mites can stay alive in ice, while quite a few insects live in hot springs above 50°C .

Homoeotherms

Homoeotherms, which maintain a constant body temperature whether the surrounding temperature is higher or lower are capable of heat regulation and maintain a heat balance. These warm blooded animals are typically land forms where heat regulation is essential and some have secondarily become aquatic and are thus, still warm blooded (otherwise all aquatic animals are

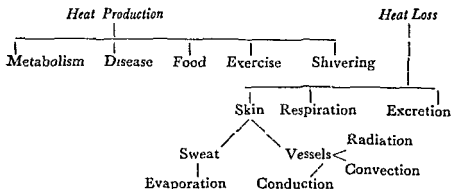
poikilotherms since water is a good conductor of heat). Thus the, homoeotherms, arctic polar bear, the tropical black bear and the brown bear, all maintain a body temperature of about 38°C . Temperature regulation is a continuous process of heat balance, between heat gained and heat lost. Heat gained is by six methods.—

- (1) increase in metabolic rate;
- (2) food supply and oxidation;
- (3) exercise *i. e.* movements;
- (4) shivering and tonus producing heat;
- (5) diseases which cause fever; and
- (6) external heat by insolation and radiation.

Heat lost is by five or more methods:

- (1) by radiation from skin;
- (2) by respiration;
- (3) by excretion through urine and excreta;
- (4) by evaporation of sweat (one gm of H_2O evaporated—means a heat loss of 536 calories of heat); and
- (5) through superficial blood vessels by conduction convection and radiation.

The Heat Balance



Adjustments of body to counteract the effects of rising temperatures are:—

- (1) increased evaporataion of water from skin, sweat; by panting from lungs and increasing the respiratory rate *e. g.* the panting and lolling of the tongue in the dog and the usual visit of

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water buffalo into water, there being no sweat glands in buffalo and only in the limb axils in the dog;

(2) vasodilation of the peripheral blood vessels of the body causing heat loss; and also raising and fluffing of feathers in birds as they have no sweat glands; and

(3) reduction of heat production by reducing exercise, large food intake *etc.*

Adjustments to counteract the effects of low temperature are:

(1) speeding up of metabolic rate, which produces more heat and may reach to *peak metabolism* (the ratio of this peak metabolism is the *metabolic quotient*);

(2) by contraction of muscles and increased exercise with shivering when temperatures are very low;

(3) increased food intake of high caloric value;

(4) vaso-constriction to reduce loss of heat,

(5) decreased or absence of sweating and lowering of respiratory rate; and

(6) development of longer and thicker fur in winter than in summer. (All arctic mammals have an alternate winter coat and summer coat). This is for insulation against the external cold, *e. g.* the Eskimo dogs have such a heavy fur that they can curl up and sleep in snow up to -30°C without increasing their metabolic rate or being affected by cold.

Arctic aquatic mammals such as seals, walruses and whales, which have no fur insulation due to aquatic habitat, have an extremely thick subcutaneous layer of fat called *blubber* for insulation against the acute cold.

All these mechanisms in homeotherms for heat regulation are controlled by a *heat regulatory centre* located in the hypothalamus, which acts as an automatic thermostat in a constant temperature room. In man it is like a clockwork, the pendulum varying between 96° and 101°F . When the body needs cooling, impulses are sent to the sweat glands causing copious sweat production. On the other hand, if the hypothalamus is cooled locally, the animal starts shivering immediately, thus producing heat.

Very small mammals, particularly in hot regions, cannot rapidly adjust their temperatures by the mechanisms mentioned

above, since heat loss by evaporation will cause dessication and death. Therefore in extremely hot climates small mammals such as rats, mice, squirrels, and kangaroo rats spend the hot day time inside burrows where humidity is higher and temperature lower than the outside.

The Kangaroo rat (*Dipodomys*) can live without drinking water (as explained in Chapter on Osmoregulation) by obtaining metabolic water from its own body. This water is used for the sparse sweating it exhibits. The camel uses up stored fluid in stomach and from hump fat for temperature regulation, although in long journeys in hot sun, its body temperature may rise from 34° to 41° C before sweating starts.

Hibernation

Almost all poikilotherms in cold regions of the world cease moving, feeding, and have a very low metabolic rate during the cold season. This is the hibernation or quiescent state caused by low temperature in most insects, snails, frogs and toads, lizards and snakes *etc.* Some fishes such as crucian carp, marinka, and some other small fishes in the north temperate region aggregate in the bottom mud and stay in a condition of suspended animation, during the acute cold winter season.

Hibernation or winter sleep is also known in some homoeotherm mammals, *e. g.* hedgehog, some squirrels, dormouse, hamster, marmot, bat and the brown bear.

All those become more or less poikilotherms during the cold winter. Their metabolic rate, respiratory rate, heart beat rate and temperature fall to extreme low levels. Growth is suppressed during hibernation. All of them store fat before the hibernation sets in, which is used as a source for the small amount of energy required to keep them just alive.

In hibernating mammals metabolism is reduced by twenty to hundred times (*e.g.* the marmot at 10° C and awake produces 2.8 KCl/kg/hour, but in hibernation or winter sleep at the same temperature it produces only 0.09 KCl/Kg/hour). In hibernating

bears the respiratory rate falls from 18 to 2/minute. Oxygen consumption may drop considerably, up to 1/100th of the normal, particularly in small mammals, *e. g.* in a hibernating dormouse the oxygen consumption lowers down to 300 ml/Kg/hour from 8000 ml/Kg/hour.

The heart slows down to a minimal rate and is even irregular below 3° C, *e. g.* the heart beat rate of an active ground squirrel is 200 to 400/minute, while that of a hibernating one is only 7 to 10/minute.

In the hamster (*Cricetus*) stimulation of the vagus during hibernation is without effect on the heart. In the hedgehog and the hamster the heart stops beating at 1.5° C and the animal awakens when air temperature drops to zero; but some individuals which do not respond actually die. The temperature of hibernating homeotherms resembles that of poikilotherms, *i. e.* the body temperature fluctuates roughly with the air temperature. Bats can possibly withstand longer and more frigid hibernation than other mammals; in temperate zones hibernation sets in from 0° C to -5° C; while tropical bats go to sleep at 8° C. In an experiment bats kept in a refrigerator for 144 days, without food or drink were capable of awakening after 15 minutes at room temperature and performed normal sustained flights.

During hibernation the endocrine glands undergo reduction, liver glycogen becomes markedly reduced and a physiological dormancy or even suspended animation sets in, and the temperature regulatory centre in the hypothalamus is set back like a clock.

Aestivation

Although taking temperature as a factor, aestivation is diametrically apposed to hibernation, it is also a state of dormancy or suspended vitality. Almost all small poikilotherms in the tropics in the hot and dry season go to rest under the mud; fishes under stones; insects, frogs and toads, lizards and snakes in crevices and holes, where they lie dormant until the extreme heat and drought

abates with the summer showers. The lung fish *Protopterus* of Africa burrows about 1 to 2 feet down into the mud and constructs a stout 'cocoon' or mudball in which it lies curled with its nares lying near the lid of the 'cocoon'. It may remain inactive in the 'cocoon' for 2 to 3 months and emerges only at the onset of rains. The twin factors of high temperature and dessication induce this aestivation. Similarly the water snail (*Pila*) can live in a condition of aestivation for years without food or water if temperature and drought conditions persist. The senior author once kept a *Pila globosa* in his laboratory drawer for four years, after which it revived on being placed in rain water. In this case the triggering mechanism for aestivation is dessication (unlike the cold temperature triggering mechanism in hibernation).

Many insects aestivate as pupae in cocoons during the hot and dry summer of the tropics *e. g.* some arthropoda, lepidoptera *etc.*

Absorption of Vitamins

Generally speaking water soluble vitamins are absorbed free, *i. e.*, after their hydrolysis. The absorption of fat soluble vitamins (A, D, E, & K) is promoted by bile salts. Although man and most animals must obtain vitamins with their food, some vitamins are synthesised by

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Absorption of Trace Elements

Magnesium and copper are absorbed in small amounts in order to keep the blood normal. Similarly, for normal functioning of organs and production of hormones, such elements as iodine, cobalt, zinc, (vanadium in ascidians) are important for metabolic processes. Although needed in minute amounts, deficiency of these trace elements often cause metabolic disturbances.

Absorption of Water

Water can be absorbed through any part of the alimentary canal in small amounts. However, the largest quantity of water is absorbed in the colon and rectum. In desert animals such as the kangaroo rat and horned toad, the only water imbibed is through their food, which consists of hard desert plants. They may live without drinking water for six months. Here, not only is almost all water re-absorbed in the large intestine and urinary tubules of the kidney, but also *metabolic water* is produced by splitting up of foods. Absorption of water moisture through skin is seen in the desert lizard *Phrynosoma* in which the skin—resembles blotting paper (as also in *Moloch horridus*).

Chapter III

METABOLISM (UTILISATION OF ABSORBED NUTRIENTS)

The nutrients absorbed through the alimentary canal are utilized for the following purposes :—

- (1) to build up new and repair broken down tissues including extra-cellular constituents and cell products, such as hormones, enzymes and other secretions;
- (2) to supply free energy, out of the bound energy, from the molecules of nutrients;
- (3) to build up reserve foods such as glycogen and fats.

Sugar metabolism (glucose, fructose, galactose and mannose)

The amounts of fructose, galactose and mannose absorbed are usually small. These hexose sugars are converted to glucose. We may thus consider the metabolism of glucose only. All hexoses can form phosphates by combining with phosphoric acid. Thus, glucose, a monosachharide, is phosphorylated and then built up into glycogen by a series of reactions.

The direction of the above-mentioned reversible reaction is determined by the needs and activities of the animal. The breakdown of glucose by a series of reactions is called glycolysis. It involves reactions of many enzymes and coenzymes and can go on in all tissues. It begins by splitting of the 6 carbon hexose molecule into 2, 3 carbon units with phosphates (Triose phosphates); and eventually each of these gives rise to a molecule of pyruvic acid. Each molecule of hexose thus gives rise to two molecules of pyruvic acid; but at the same time it has lost four hydrogen atoms, which

are taken up by hydrogen acceptors (such as coenzyme I) which are consequently reduced. In muscles, when oxygen is absent, the hydrogen is taken up to reduce pyruvic acid into lactic acid. This lactic acid is then carried away by the blood, and in the liver the oxidation of 1/5th part of it supplies enough energy for the resynthesis of lactic acid into glycogen (Fig. 32). Glycolysis probably accounts for more than 90% of the oxidation of glucose in mammals. If any hydrogen atoms are left unaccepted, they are removed by coenzyme II. The reactions can be expressed as follows:—

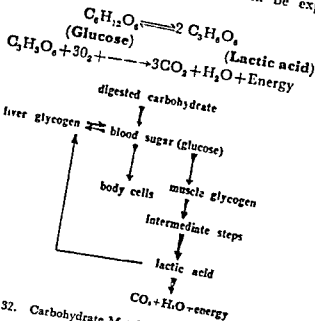


Fig. 32. Carbohydrate Metabolism the body.

A balance sheet can be set-up to show the energies liberated by oxidation of Glycogen and lactic acid :

1 gm glycogen when burnt liberates.....4,000 cal.

1 gm lactic acid when burnt liberates.....3,600 cal.

conversion of 1 gm of glycogen to lactic acid requires..400 cal.

The normal value for *blood sugar* (glucose) in man is about 80 mg/100 ml. of blood, distributed equally between corpuscles and plasma. A normal man can take upto 150 grams of glucose

without glycosuria (sugar in urine). If higher amounts of glucose are injected into the blood, hyperglycaemia results. This is also true of patients suffering from diabetes, in which the hormone insulin is low or absent. If excess of insulin is injected into a hyperglycaemia patient the blood sugar may become sub-normal (hypoglycaemia) and cause death.

All Vertebrates appear similar in carbohydrate metabolism, although they differ in some details. The blood sugar of birds is about twice that of mammals, which is connected with the paucity of L cells and richness of β cells in the pancreas. This hyperglycaemia is useful for providing ready energy in active flight.

Glycogen is the main stored carbohydrate in all vertebrates; but it is present also in some invertebrates such as Pelomyxa (protozoan), the peritoneum of earthworms (annelida), the connective tissue and gonads of molluscs and the digestive diverticula of crustacea. Helix pomatia, (a snail) contains another reserve carbohydrate galactogen, which is similar to glycogen, but is not attacked by amylase. On acid hydrolysis galactogen yields galactose instead of glucose.

One peculiar characteristic of glycogen is the fact that it can produce, by partial decomposition, such compounds which give rise to fats, the reaction steps of which are incompletely known. It is a time-old practice to fatten cattle by feeding with glycogenic compounds. Thus, when a hog is fed on corn (which is almost entirely starch) it gets fattened on it.

Protein Metabolism

Proteins are synthesised from absorbed amino-acids. It has been shown by using radioisotope labelled nitrogen, that the complete formation of a protein molecule from its constituent amino-acid blocks may take as much as 25 minutes.

Many of the amino-acid molecules absorbed through the gut go through a series of processes, in which nitrogen is removed and ultimately excreted, the remainder being made available for other uses. This is because protein nitrogen digested in animals is

... amino acids needed for the synthesis of body proteins
... and growth. It is especially true of carnivores. The

... but deamination only occurs rapidly in liver and kidney.
In transamination the amino-group is exchanged for the keto-
group of a keto-acid; while in deamination there is an oxidation
which removes the nitrogen as ammonia. This ammonia is excre-
... but in terrestrial animals further
(See Chapter on Excretion)

The non-nitrogen parts of the amino-acid or keto-acid mole-
cules, ultimately help in providing energy for the animal by
oxidation.

Some amino-acids in addition to serving as building blocks of
body proteins have also a protective function. They combine with

Some
is also
true for cells in general.

... (like the gene pools
of the species and the
pools, the amino-acid pools seem to be larger for higher animals
than for lower ones.

Little is known of nitrogen metabolism in invertebrates.
Possibly the separation of ammonia from amino acids is done as in
vertebrates, by deamination process.

vertebrates). The greater part of the fat is stored as adipose subcutaneous and intramuscular fat. This fat can be available to the tissues as and when required. A small amount of fat (*constant fat*) remains always deposited in the brain, heart, lungs and kidneys, and stays there even during starvation. Thus, constant fat is never removed or oxidised for energy production.

Stored fat is not inert as ordinarily supposed. There is a continuous decomposition resynthesis, and inter-conversion. Fatty acids undergo a process called β oxidation by a series of reactions involving several enzymes and coenzymes.

The chain of the fatty acid loses some carbon atoms repeatedly with gradual shortening of the chain. The glycerol derived from fats is oxidized, with ATP, as a coenzyme to triose phosphate. This may either be oxidised through the tricarboxylic acid cycle or synthesized to glucose or glycogen. Certain fatty acids *viz.* linoleic and arachidonic acids are now considered as essential fatty acids. Deficiency symptoms such as scaly skin, renal lesions and abortions develop if they are completely absent from the diet.

Cold-blooded animals such as fish and frog tend to have a higher proportion of unsaturated fats than the birds and mammals. Cold region animals as a rule, have higher percentage of fats than animals of the warm regions.

Vitamin and Mineral Metabolism

The importance of vitamins in prevention of diseases and the formation of a part of some enzymes is well known. For example, the carboxylases are not active enzymes unless they are combined with thiamine (vit. B₁ the anti beri-beri vitamin). Similarly, Riboflavin (vit. B₂) is required in some coenzymes. The role of vitamin A in the production of visual purple is well known.

Inorganic substances absorbed by the gut are essential for a host of bodily functions. Calcium carbonate, calcium phosphate calcify the organic matrix of bones in vertebrates. Surprisingly, calcification is a reversible process and decalcification outbalances

calcification, if calcium salts are lacking in the diet. Salts (specially chlorides) are essential for the maintenance of osmotic pressure of the body fluids.

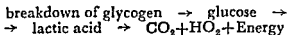
Besides, there are specific effects of some metallic ions. For example, excess of calcium causes tetanus and calcium rigor of the heart. Calcium, however, is indispensable for the clotting of blood. A blood sample can be prevented from clotting by the addition of over 1% potassium, ammonium or sodium oxalate, which causes the precipitation of calcium in blood, thereby preventing clotting. Phosphorus is required for phospholipids and phosphorylation; while iron is essential for haemoglobin. Deficiency of iodine causes hyperthyroidism (*goitre*) since it forms an essential part of thyroxine. Some trace elements such as manganese, cobalt, and zinc, act as catalytic agents of enzymes and their reactions.

Anaerobic Metabolism

Most endoparasites have *anaerobic metabolism* of carbohydrates as the source of energy. Anaerobic metabolism of carbohydrates leads to the formation, not only of lactic-acid, but also of fatty acids, such as pyruvic, succinic, valeric and higher fatty acids. For example, valeric acid is produced by *Ascaris*; higher fatty acids by *Fasciola*. Anaemia in man, caused by helminth infections, has been found to be due to the accumulation of these fatty acids, which retard or reduce the production of haemoglobin. Some protozoan parasites, such as a malarial parasite (*Plasmodium*) have a Krebs's cycle; where others such as *Trypanosoma* do not have it.

Most micro-organisms obtain the metabolic energy from glycolysis or partial breakdown of absorbed food molecules without any oxygen. In fact it is believed that the first living organisms on earth were anaerobic, due to the virtual absence of free oxygen in earth's atmosphere. Oxygen was later produced as a by-product of photosynthesis by green plants after which aerobic metabolism became common in the animal world. Aerobic meta-

bolism is certainly superior to an aerobic type, since the energy obtained ;



is much more than by breakdown of glucose into lactic acid anaerobically.

Basal Metabolic Rates

The basal metabolic rates (BMR) of different animals are determined by the amount of oxygen used per gram of body weight per hour. These are given in detail in the Chapter on Respiration.

Hibernation.—(Hedgehog, squirrels, dormouse, hamster, marmot, and bat) :

- (1) Homootherms become poikilothermous during cold season, at about 5° C.
- (2) Temperature and heart beat rate fall to very low levels.
- (3) Animals deposit fat during summer, the deposited *fat* being used as a source of energy.
- (4) Several endocrine glands show involution and consequent fall in BMR.
- (5) Stop feeding (fasting).
- (6) *Brown bear* spends winter in dormant state ; but not typical hibernation ; since no striking fall of temperature or heart beat ; only polar bears hibernate.
- (7) *Bats*—poikilothermus when not in flight, irrespective of season ; hibernate in all cold countries.

Chapter IV

RESPIRATION (RESPIRATORY SYSTEM)

Respiration

change of oxygen and carbon dioxide through special respiratory organs, viz. gills, tracheae, book lungs and lungs (Fig. 33). In

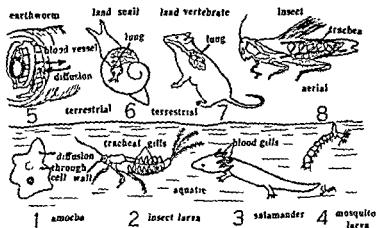


Fig. 33. Different types of respiratory mechanisms in aquatic, terrestrial and aerial animals.

some lower animals (e. g. protozoans, coelenterates, and annelids) there are no special respiratory organs, but sufficient oxygen for respiration is obtained by diffusion through general surface of the body. Internal or cellular respiration is the release of energy inside the tissue by oxidation of glucose and lactic acid. In the tissues

mm; whereas in CO_2 , 40 mm.

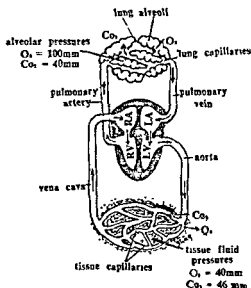


Fig. 34. Diagrammatic representation of interchange of gases in lungs and tissues.

Oxygen makes up 20.95 percent of air; the rest is nitrogen, argon, and carbon dioxide. At sea level, the partial pressure of oxygen is 159 mm and is soluble

in water, the amount dissolved depending on concentration of oxygen in air, temperature and pressure. It is important to note that all respiratory exchange is through an aquatic medium, whether the animal is aquatic or terrestrial. If the lungs even in mammals become dry no respiratory exchange can take place.

One ml of oxygen is dissolved in 100 ml of water at 0.8°C . with increasing temperatures the solubility decreases, *e. g.* at 15°C there is only 0.7 ml of O_2 per 100 ml of water; and 37°C the solubility is reduced to 0.5 ml of O_2 per 100 ml of water.

With an increase in atmospheric pressure more O_2 is dissolved in the water. The normal atmospheric pressure at sea level is 760 mm and the partial pressure of O_2 is 159 mm. We can then say

that 159 mm is the *tension* of oxygen in water. In other words the tension of a gas in solution is equal to the partial pressure of the gas in the atmosphere in equilibrium with the solution. This holds true in lung respiration as well. Since oxygen take up in the lung is by diffusion in to the blood till the O_2 tension of blood is equal to that of the lung (Fig 35). With increase in altitude the

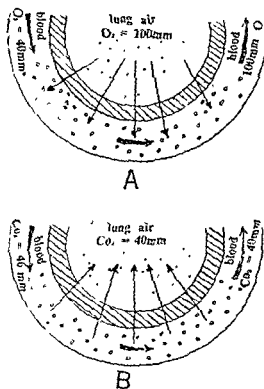


Fig. 35. A. Gaseous exchange in the lung.

oxygen concentration decreases in proportion with the decrease in atmospheric pressure. Thus, at 18,000 feet the atmospheric pressure is one half that of sea level and amount of dissolved oxygen is also one half.

Carbon dioxide, which is given out or expired in respiration is about 30 times as soluble in water as oxygen and it forms H_2CO_3 in water.

in osmoregulation.

Nitrogen is less soluble in water than oxygen and thus it is given off quicker than oxygen if pressure is reduced. Nitrogen plays no physiological role, being an inert gas. However, in special circumstances it is of great importance. If a man is exposed to sudden reduction in pressure, as an astronaut ascending in the sky in a non-pressurised capsule, his blood may become filled with nitrogen bubbles due to sudden reduction of atmospheric pressure. In the same way when a diver is under compression, under the sea and is suddenly raised to the surface, there is again release of nitrogen bubbles in the fine blood vessels causing decompression sickness, and blocking of nerves (as happened to J. B. S. Haldane, F. R. S. in his experiments) often with fatal results.

External expiration (Exchange of gases in water or air)

GENERAL BODY SURFACE

As already stated small animals e. g. protozoa require a small amount of O_2 and gaseous exchange takes place through general surface of the body. This is also true of somewhat larger animals, such as coelenterates and annelids, which are sluggish and do not have a high rate of oxygen consumption.

surface of the body, diffusion taking place through solution.

(2) GILLS

In large aquatic animals in which the skin is almost impermeable to respiratory gases gills arise for respiration.

Three major groups of aquatic

gills viz. crustacea, mollusca and

many larvae such as those of may flies, lung fishes, salamanders as also early tadpole of frogs have unprotected external gills.

In Cray fishs, lobsters, crabs etc. (crustacea) the gills are relatively large and covered by a chitinous external skeleton

(Fig. 36). In molluscs the gills lie inside the mantle cavity, which again is covered by a hard shell. The water is circulated over the large surface area of the gill folds by the beating of

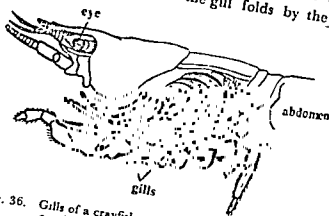


Fig. 36. Gills of a crayfish as seen after the removal of exoskeleton.
(After T. H. Huxley)

millions of cilia covering the surface of the gills and lining of the mantle cavity. In the squid and Octopus, the walls of the mantle cavity are muscular and actively pump water in and out, ventilating the gills.

Among vertebrates aquatic respiration is most highly developed in fishes. In cyclostomes and sharks the gill slits are exposed, water flowing in (incurrent) through the mouth and going out through the gill slits (excurrent). In bony fishes (Fig 37), a hard operculum covers the gills, with an opercular opening on each side through which the excurrent goes out. The fish opens and closes its mouth, thus driving the incurrent into the opercular chamber, the back flow being prevented by oral valves. Similarly, an opercular valve allows the excurrent only to flow out wards. This can be compared to a force pump. It may be noted that fish gills can not respire air due to the collapse of gill filaments when out of water.

SOME GILL MODIFICATIONS FOR AQUATIC RESPIRATION

The external gill filaments of some marine worms (*Arenicola*), the larvae of lung-fishes and salamanders as well as the

early tadpole of frogs can be called blood gills, since the large

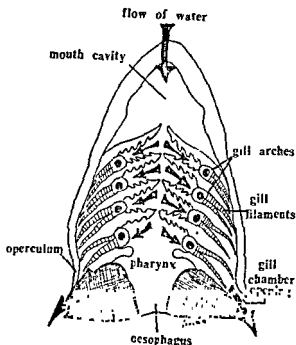


Fig. 37. Dissection of head of a bony fish to show the mouth cavity and gills. (Modified after Norman)

number of slender gill filaments covered by delicate epidermis

ward

some

esent

(Zygoptere, and a

few Lepidoptera), as leaf-like appendages containing large num-

bers of superficial tracheoles under a permeable covering. A-

peculiar type of aquatic respiration by gills is found in the king

ntaining

These

oxide in

water.

Another peculiar mode of aquatic respiration is the anal respi-
ration of some polychaetes and an ascending ciliary current

ing into the rectum assisted by antiperistalsis. Similarly, dragon-fly nymphs have rectal tracheal gills, water being pumped in and

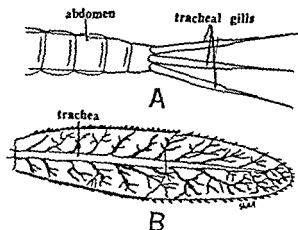


Fig. 38 Tracheal gills of larval zygoptera.
A—Dorsal view;
B—Lateral view of one lamella.
(After Tillyard)

out of the rectum. On the other hand the entire holothuroidea breathe by cloacal respiratory trees with branched vascular diverticula, (The fish Fierasfer lives temporarily in the cloaca of holothurians and thus obtains more oxygen). Among the vertebrates some tortoises pump water in and out of the cloaca for respiration (anal respiration)

3. TRACHEAE

All adult insects and a few other arthropods have a highly specialized respiratory system, in which instead of blood vessels carrying the oxygen to different parts of the body in solution, air is directly carried to the tissues by a branching system of tubes called tracheae. The tracheae carry oxygen (in air) through paired openings called spiracles. Repeated branching of the tracheae to form tracheoles, less than one thousandth of a millimeter (μ) in diameter, ramifying to every part of the insect's body; in some cases, the tracheae branch into even finer tubes. (Fig. 39)

The ded

form an air tube on water film or to filter out dust particles in air

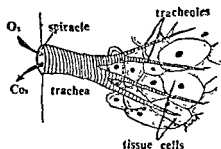


Fig. 39. In insects, the tracheoles bring oxygen direct to the tissue cells (semi-diagrammatic).

(Fig. 40). Thus, in insects, blood is not needed for carrying oxygen and carbon dioxide

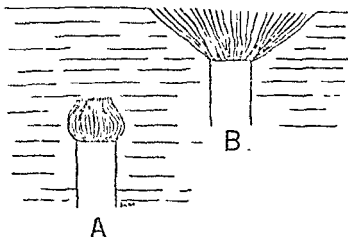


Fig. 40. Movements of hydrophilic hairs surrounding a spiracle
 A—Insect submerged : hairs close over spiracle preventing entry of water.
 B—Insect surfaced : hairs separated by surface tension exposing the spiracle to air. (After Chapman)

Some insects (e. g. mosquito larvae) have posterior air tubes or respiratory siphons, which draw in air at surface of water and allow the larva to stay under water. A peculiar adaptation of the respiratory siphon is seen in the larva of *Eristalis* fly in which there is a posterior telescopic siphon which can be drawn in and out

(according to the depth of the water in which it lies) to keep the terminal spiracle above the water surface for aerial respiration (Fig. 41).

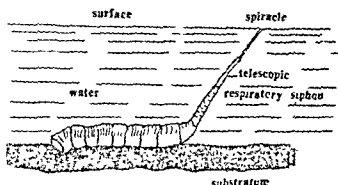


Fig. 41. Larva of *Eristales* with telescopic respiratory siphon.
(After 1 mm.)

4. BOOK LUNGS

All arachnids (spiders and scorpions; ticks and mites) have a peculiar system of respiratory organs called book lungs. There are four pairs of book lungs in scorpions and one to two pairs in spiders. Each book lung contains a large number of leaf like horizontal plates arranged as the leaves in a book, containing fine blood vessels. Air enters through an external slit guarded by a valve plates, where oxygen

5. VERTEBRATE LUNGS AND AERIAL RESPIRATION

Some fishes have both aquatic and aerial respiration.

in *Anabas*, air-sacs in *Heteropneustes* and arborescent organ in *Clarias*. All these fishes have both aquatic and aerial respiration; since they have to survive shorter or long periods in air when water is

foul (without oxygen) or has evaporated from streams and pools in hot and arid climates. The African lung fish Protopterus is

Amphibia (which are amphibious in habit) have three types of respiration, viz. cutaneous (in water) buccal and pulmonary (on land). The lungs have no mechanism of their own to force air

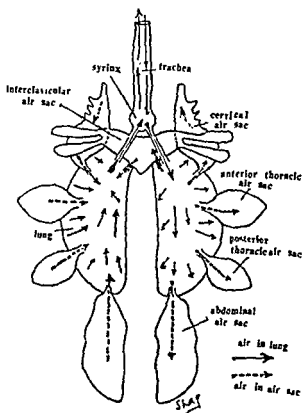


Fig. 42. Double respiration in birds (diagrammatic). Solid arrows indicate passage of tracheal air in and out of lungs (first respiration); broken arrows show the passage of lung air in and out of air sacs (second respiration).

in and out. The inspiration and expiration is accomplished by a

buccal force pump, similar to the one described in aquatic respiration of fishes. The structure of lungs is also similar to that of the air bladder in fishes, containing only *sacculi* and *alveoli*.

Reptiles have similar lungs but the internal folds are highly convoluted to form *sacculi*, *alveoli* and *infundibuli*. In birds breathing is highly efficient, as there is *double respiration* (Fig. 42). Air is inspired right through the *first respiration* takes place. The *alveoli* and are non-respiratory, air through the *alveoli* of the lungs. This may be called a *second respiration*. In water birds such as ducks and geese there is a reflex which produces stoppage of breathing (*apnoea*) when their heads are under water.

In mammalian lung there is an additional large chamber, called the *atrium* into which the terminal *branchioles* end (Fig. 43).

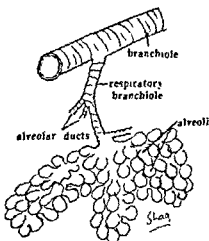


Fig. 43. Atria and alveolia in the lung of a mammals,

External respiration in mammals has been studied most
r that moves in or out with
At rest the tidal volume

is about 500 mls; but the total capacity called vital capacity when lungs are freely distended, is about 4,000 mls (4 litres). Athletes often have a much higher vital capacity (upto 6 litres or more) some air is always left behind in the lungs after expiration. This is called residual volume, which is about 1,500 mls (1.5 litres). The amount of fresh air taken into the lungs is about 10 litre per minute, at rest the respiratory rate being about 20 per minute.

MECHANISM AND REGULATION OF PULMONARY RESPIRATION IN MAMMALS

Respiration is brought about by diaphragm and respiratory muscles (external and intercostals). Inspiration is effected: (i) by an antero-posterior enlargement in size of the thoracic cavity caused by contraction and straightening of the diaphragm; (ii) by an enlargement caused by the action of external inter-costal muscles which pull the rib cage outwards. The negative pressure thus caused in the pleural cavities brings about expansion of lungs, causing a lowering of pressure below the atmospheric pressure. Air thus rushes into the lungs until intra-pulmonary pressure equals atmospheric pressure.

Expiration is effected by decreasing the thoracic cavity: (i) by the action of elastic forces (elastic recoil); (ii) by reduction of the negative pressure in the pleural cavities caused by contraction of inter-costal muscles. The intra-pulmonary air is thus compressed until its pressure rises above the atmospheric pressure when it is forced out of the lungs. Expiration continues until intra-pulmonary pressure equals atmospheric pressure.

Regulation of respiration is performed by six types of neural mechanisms:—

(1) the medullary respiratory centre (MRC) controls it: (a) by afferent nerve impulses; and (b) by chemical influences which effect it directly or indirectly.

(2) The neurons which descend from the respiratory centre into the spinal cord to synapse with the efferent neurons of the respiratory muscles.

(3) The efferent nerves (*viz.* the phrenic and inter-costal nerves) directly supplying the respiratory muscles.

(4) The pneumotaxic centre acts as an inhibitory mechanism to interrupt discharge of medullary respiratory centre messages.

(5) The Hering-Breuer vagal reflex mechanism also inhabits the respiratory centre. It accelerates the rate and reduces the depth of respiratory movements.

(6) Afferent nerves from the carotid sinuses, aortic arch, carotid and aortic bodies *etc.*, which contain chemoreceptors, are stimulated by: (a) decrease in arterial O_2 tension; (b) increase in arterial CO_2 tension; and (c) increase in H ion concentration in arterial blood.

The main regulation of respiration is thus performed by the medullary respiratory centre (MRC), which is located in the medulla oblongata. It is bilateral, each half being composed of both an inspiratory and an expiratory centre. The MRC is constantly under direct chemical control, the predominant factor being the CO_2 tension of the arterial blood. An increase in CO_2 tension accelerates respiratory movements, while a decrease depresses this centre reducing the respiratory rate.

Thus, the rate and depth of breathing vary directly (within limits) to the rate of CO_2 production by the cells of the body; so that the volume of air breathed at any period is determined largely by the actual demand for oxygen. This is remarkably seen in aviators and divers. If an aviator goes up 20,000 feet, his rate of respiration will keep falling, in spite of the fact that his body is in acute want of oxygen. This happens since with rarification of air the CO_2 content is radically lowered and there is a decrease in the stimulation of respiratory centre by CO_2 . Thus, he may die due to lack of oxygen. On the other hand, the diver with compressed air under the sea has a high amount of O_2 to breath as his respiratory rate increases due to high CO_2 content stimulating the MRC. Thus, he may succumb to high oxidation or burning of tissues. We see thus that CO_2 is more important than O_2 in regulating respiration. If the amount of CO_2 in inhaled air is increased by a few percent,

the ventilation of the lungs is more than doubled, but a decrease in O_2 by a few percent has no effect whatsoever on the respiration rates (Fig. 44).

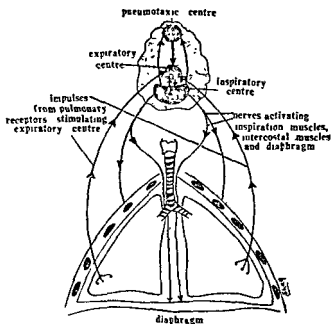


Fig. 44. Medullary respiratory centre for control of respiratory rate. (Arrows indicate the direction of nerve impulses).

RESPIRATION IN AQUATIC MAMMALS

In aquatic and diving mammals such as seals, porpoises, whales *etc.*, there is a surprising cessation of respiration from ten minutes in the seal to two hours in the large whales. The oxygen lack during this submergence period is compensated in the following ways:—

1. The lungs are enormously larger than similar sized land animals.
2. There is an enlargement of some veins into venous sinuses which store oxygenated blood for use under water.
3. The heart beat falls in the seals from 150 per minute to 10 per minute. The rate of circulation is thus reduced and little lactic acid or CO_2 enter the blood from the muscles.

4. There is a high content of myoglobin (muscle haemoglobin) which carries oxygen in the whale and the seal for use under water.

5. There is a fall in body temperature (aided by a fall in temperature of deep waters) lowering the body metabolism, and thus less oxygen is required.

6. During the diving period (apnoea), anaerobic respiration occurs to some extent, viz., conversion of glucose into lactic acid.

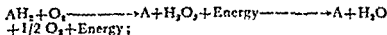
In all diving mammals that have been investigated an oxygen debt is built up which has to be paid back when the animal surfaces to breathe again. The oxygen debt is due to: (a) using up of oxygen from haemoglobin in the blood and in myoglobin, (b) the lactic acid mechanism.

The whale surfaces from half to two hours of diving or sounding and exhales by characteristic *sputting* in a column of vapour and spray. Next it inhales up to the vital capacity of lungs and sounds again. Although the whales are air breathers they are often found stranded and dead on sea shores. This is because once beached out of water, the upthrust of sea water disappears; and the enormous weight of its body collapses and crushes its lungs. Thus, it cannot respire air on land as the smaller seals and porpoises can do.

INTERNAL OR CELLULAR RESPIRATION

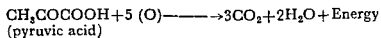
..... from the

The molecules of different foods absorbed (*metabolites*) are broken down by oxidation and step wise enzyme-catalysed reactions. Energy contained in metabolites is freed by their oxidation which can be summarised by the equation:—



in which AH_2 stands for oxidizable substrate, the oxidation consisting of removal of hydrogen. The early stages of the oxidation of a substrate are anaerobic and only in the last stage is

oxygen involved as acceptor of hydrogen. For example, in the
 being :



In internal respiration the actual breakdown of pyruvic acid involves a complicated series of reactions known as Kreb's cycle (Fig. 45), which require a number of enzymes and coenzymes.

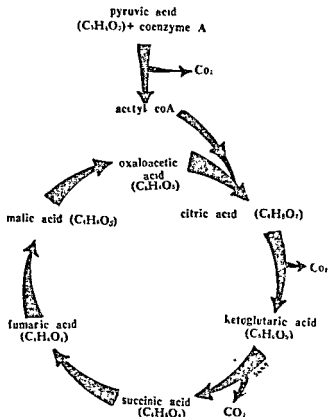
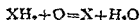


Fig. 45. Stages in the kreb's (Pyruvic—citric acid) cycle.

A typical dehydrogenation can be represented by the reaction :

dehydrogenese

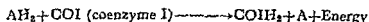
$AH_2 + X \rightleftharpoons A + XH_2$, where AH_2 is the original substrate, X the hydrogen carries, A the oxidised substrate and XH_2 the reduced carrier. This reduced carrier or with a second carrier which possess greater affinity for hydrogen, *e. g.* :



or

$XH_2 + XI = X + XIH$ (X being first carrier and XI being second carrier).

A typical example of hydrogen carrier is coenzyme I, which



The reduced coenzyme I can again be reoxidised. Dehydrogenisers or hydrogen carriers are found in the cells of all animals as coenzyme I, cytochromes *etc.*, (coenzyme I being Adenine—nicotin amide—ribose phosphoric acid; the cytochrome is a haem—nitrogen base compound universally present in oxygen using tissues—the respiratory rate of a cell is almost proportional to its cytochrome content).

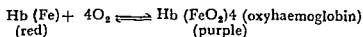
RESPIRATORY PIGMENTS

apply in the internal respiration. haemoglobin (red blood); haemocyanin (blue blood); haemerythrin (violet blood); and chlorocruorin (green blood). Such fluids may not be contained in blood vessels but as general body fluids. Oxygen is transported in a combined state which these respiratory pigments and is never carried free. Haemoglobin is found in some invertebrates and all vertebrates; haemocyanin in crustaceans and molluscs, haemerythrin in some annelids, and chlorocruorin in many polychaetes.

RESPIRATORY PIGMENTS

Pigment	Metal present	Colour		Animal groups where present
		Oxyge-nated	Deoxyge-nated	
Haemoglobin	Iron	Red	Red	Vertebrates and scattered invertebrates
Chlorocruorin	Iron	Green	Green	Some poly-chaeta
Haemerythrin	Iron	Red	Colourless	Some annelids
Haemocyanin	Copper	Blue	Colourless	Most molluscs and arthropods

Haemoglobin (as also the other respiratory pigments) are protein compounds of metals, acting as carriers of oxygen, *e. g.* :



Taking haemoglobin [molecular weight—68,000; molecular formula— $(C_{712}H_{1330}O_{244}N_{214}S_2Fe)_4$] as an oxygen carrier it is known that oxygen is carried in the form of O_2 with ferrous iron, Fe^{2+} , per atom of Fe^{2+} . If ferrous iron is changed to ferric by strong oxidizers then the stable methhaemoglobin is formed, which is incapable of combining with oxygen.

The equilibrium situation in cellular respiration depends upon the O_2 concentration in blood, which in turn depends on the O_2 tension in blood. The *tension of loading* in blood is that O_2 tension (as partial pressure) at which the blood is 95% saturated

with O_2 . On the other hand the *tension of unloading* is that tension at which the blood is only 50% saturated.

In the tissues where oxygen is used for oxidation (*katabolism*) the O_2 tension is more than in the air bathing the alveoli of the lungs. Hence by the law of partial pressures the O_2 tension need not go below 50 mm to liberate half the oxygen from the blood.

There is a decrease in the affinity of haemoglobin for oxygen in presence of CO_2 and this is of great use, since it increases the amount of O_2 liberated in the tissues.

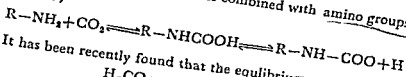
Ordinarily the haemoglobin of the erythrocytes carries about 20 volumes of oxygen per 100 volume of blood, the plasma carrying only a negligible amount of O_2 . **Individual tissue cells receive the oxygen through lymph and not directly by blood**, which remains only in the blood capillaries normally.

After oxidation and consumption of oxygen by tissues, CO_2 is produced in the cells. This CO_2 dissolves freely in the tissue fluids (lymph) surrounding the cells and passes thence into the plasma within the blood capillaries. CO_2 is also not transported free but in a combined state in three different ways:—

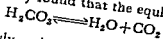
(1) 80% of the CO_2 in blood is carried as bicarbonates i. e.
 $CO_2 + H_2O \longrightarrow H_2CO_3; H_2CO_3 \rightleftharpoons H^+ + HCO_3^-$

(2) 10% of the CO_2 in blood is bound as carbonates.

(3) 10% of the CO_2 in blood is combined with amino groups, viz;



It has been recently found that the equilibrium

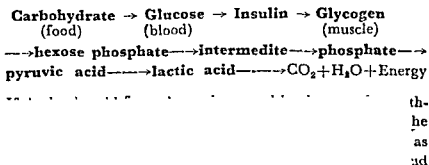


is reached very slowly, whereas the exchange of CO_2 between tissues and plasma is very rapid. How does this happen? This is done by the presence of an enzyme, carbonic anhydrase, which

catalyses the reaction. Finally plasma carries all CO_2 to the lungs for gaseous exchange.

What is the source of CO_2 in cellular respiration? The

immediate source is lactic acid, which is being continuously formed, during work, associated with release of energy in the following steps:—



RESPIRATORY QUOTIENT

Respiratory quotient (RQ) is a calculated measure to express the ratio between the volume of CO_2 given out in a definite time and the volume of O_2 absorbed in the same time under the same condition. It may be expressed as:—

$$\text{R. Q.} = \frac{\text{Volume of } \text{CO}_2 \text{ given out in time T}}{\text{Volume of } \text{O}_2 \text{ absorbed in time t}}$$

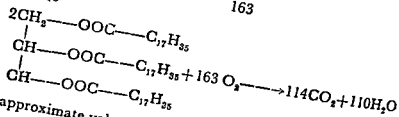
Since the volume of a gas, under given condition of temperature and pressure is proportional to the number of molecules it contains, it is easy to calculate the theoretical value for the chief classes of food stuffs (assuming complete oxidation).

For all carbohydrates the equation is



in which case it is obvious that R. Q. is one.

The fat Tristearin has an R. Q. $\frac{114}{163}$
or 0.70, since



The approximate value for the quantity of protein broken down in a given time can be obtained from the nitrogen excreted in the urine. And if the volumes of O_2 taken up and CO_2 produced are known, the amounts of these concerned with protein metabolism can also be calculated. Thus, from carbohydrate, fat and protein metabolism the total energy production by internal respiration can be calculated although what has been measured are only O_2 , CO_2 and N_2 .

Basal Metabolic Rate (BMR)

The form and intensity of activities in an animal vary with environmental temperature, phase of growth, reproduction and exercise. Such variations can be excluded or minimised and a basal rate of metabolism obtained for each animal individual or species. During the estimation of BMR it is ensured that:—

1. the environmental temperature is within the thermal neutrality range (no regulatory effort is required on the part of the subject);
2. the animal should be completely at rest during the estimation of BMR (even processes like ingestion, digestion and excretion are ruled out).

The quantity of energy required in a unit time, under standard basic conditions, with only basic vital activities continuing, is called the Basal Metabolic Rate (BMR).

But how can this be measured? All energy release is associated with some production of heat dissipated by the animal in unit time is measured and is one of the methods of estimating

BMR (In an average man it is 40 Calories per square meter body surface per hour, 37.5 cal/sq m body surface hour in an average woman).

The best method for estimating BMR at the present time is the experimental estimation of the amount of oxygen utilized for energy release. BMR then usually means rate of oxygen consumption by an animal at rest. The oxygen consumption is estimated by the removal or absorption by alkali of CO_2 produced in respiration.

Sedentary animals such as sea-anemones and sand-worms have O_2 consumption in mm^3 per gram body weight per hour (BMR) hardly 13 to 30. The trout has a BMR of 226, while man has a lower BMR of about 200.

As a rule smaller the animal, the higher the BMR but the same sized animals may differ in BMR due to difference in activity.

METABOLIC RATES OF DIFFERENT MAMMALS

Body weight (gms)		Oxygen consumption ($\text{mm}^3/\text{gm. hour}$)
Mouse	25	1,580
Rat	226	872
Rabbit	2,200	466
Dog	11,700	318
Man	70,000	202
Horse	7,00,000	106
Elephant	38,00,000	67

Chapter V

CIRCULATION (CIRCULATORY SYSTEM)

Protozoa and the simple metazoa (*e. g.* sponges, corals, jelly fishes *etc.*) have no vessels for transport of internal fluids. Some of them however, have passages or cavities in which movements of external fluids (sea or fresh water) takes place. That, there is no need of a closed vascular system in the lower invertebrates is illustrated by the flat-worms (Turbellaria), in which the inner-most cells are brought close to the epithelium by the worms flatness itself, so that gaseous exchange can easily take place. Also, there is no need for circulation of food products from the gut, since there is an elaborate branching of the gut and no internal tissue is far from the gut branches.

Some multicellular animals have internal spaces or cavities between the body wall and alimentary canal (**Coelom**) containing a fluid (**coelomic fluid**) used as a transport system. The first group of animals to have a **closed system** of blood vessels is Annelida (earthworms, leeches *etc.*) where vessels branch into *capillary networks*, in tissues, and organs of nutrition and respiration. Such an arrangement is to be found in all vertebrates. Since the circulatory fluid has to be *forced* through the vessels, a system of **valves** keeps the direction of circulation constant. The propelling organs are called **hearts** in all animals, which may however differ in number, arrangement and structure. The common earthworm, for example, has 8 pumping hearts, around the front part of the alimentary canal. The leech has two lateral contractile vessels comparable to hearts. Similarly there are 13 hearts in cockroach for pumping the haemocoelomic fluid. The arthropods have an **open vascular system**. Here the blood is discharged from and into spacious

sinuses in the tissues. In all cases of circulation, however, the flow of the circulatory fluid being in one direction, it follows that this fluid must eventually return to the heart and must somehow make a complete circuit (**circulation**) of the body.

There are three types of circulatory fluids: **blood, lymph and haemocoelomic fluid**. In the lower animals some of these fluids may be combined, but in higher animals there are usually two separate systems, one for the blood and the other for the lymph. There may even be separate *lymph hearts* to drive the lymph.

Direction of Blood Flow

The unidirectional vascular circuit is ensured by a combination of the following mechanisms:—

(1) **The antero-posterior asymmetry of blood : vessels**. Generally a median vessel is broad at the anterior end and tapers posteriorly. This means less volume of blood in posterior than in anterior allowing easier contraction (in which less force is needed) of the posterior part. Thus waves of contraction begin at posterior end pushing the blood forward, as in the shore-worm and the earth-worm.

(2) **The Position of Pace-Maker Mechanisms** (centres of automatic stimulation for contraction). These are usually situated at one end of the active stretch of the contractile vessel or heart. By this mechanism, the wave of contraction can spread only in one direction from that end towards the other end.

In ascidians (*e. g. Ascidia, Herdmania*) the tubular heart is supplied with three pace maker centres, one at the middle and one at each end. The two terminal centres act alternately, and therefore the direction of blood flow is changed after a few heart beats. This is the only example of **reversal of circulation** in the whole animal kingdom.

(3) **Sub-division of Heart into Chambers**: Such an arrangement is common in most invertebrates. These subdivisions are located serially and contraction of one chamber causes dilatation of the next chamber. The succession of contraction of these chambers, thus decides the direction of flow. This is also true for simple vertebrate hearts (in cyclostomes and fishes).

In the invertebrates, as well as the lower vertebrates, there is no separation of arterial (oxygenated) and venous (deoxygenated) bloods. However, vertebrates with the separation of the auricle into two halves and the ventricle into a right and a left chamber, the two bloods become separated. This is so in some reptiles (crocodiles) and birds and finally in the mammals (Fig. 46). Here the venous blood is collected in the right auricle

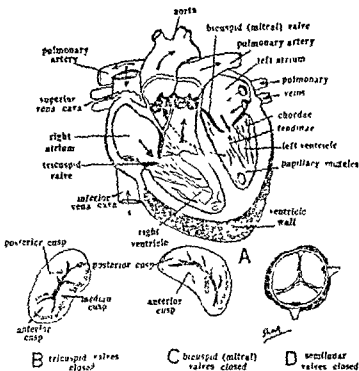


Fig. 46. A—Structure of human heart as seen in a sagittal section. B to D—Action of heart valves. (Arrows indicate the path of blood).

passed into the right ventricle and then transported into the lungs through the pulmonary arteries, for oxygenation. This is the first passage of blood through the heart. The same blood after oxygenation is returned to the left auricle and then to the left ventricle, to be pumped into the entire body through the aortic arch. This is thus the second passage of the same blood through

the heart in one cycle through the body. Since the same blood

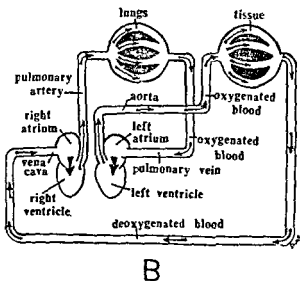
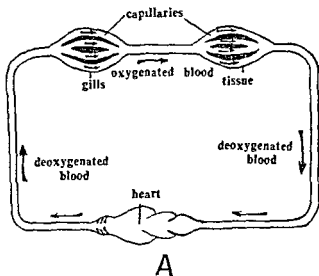


Fig. 47. A—Single circulation in which the blood passes only *once* through the heart during each circulation.
B—Double circulation in which the blood passes through the heart *twice* during each circulation.

passes two times via the heart, in one cardiac cycle the circulation is termed **double circulation** in these animals (Figs. 47).

(4) Special Sphincters and Valves These are present not only

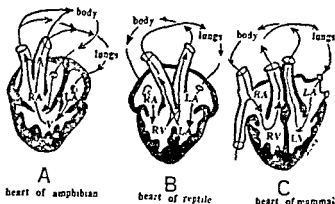


Fig. 48. Diagrammatic representation of circulation of blood through heart:—

A—Heart of Amphibian : Oxygenated blood gets partly mixed with de-oxygenated blood, there being a single ventricle.

B—Heart of Reptile : Ventricle is incompletely partitioned, preventing the mixing of blood to a large extent.

C—Heart of Mammal (and Bird) : Ventricle is completely partitioned, preventing any mixing of oxygenated and de-oxygenated blood.

(R. A.—Right auricle ; L. A.—Left auricle ; R. V.—Right ventricle , L. V.—Left ventricle ; V—Ventricle).

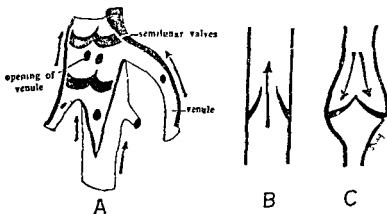


Fig. 49. Valves in veins and their action (arrows indicate the direction of blood-flow).

A—A vein cut open to show pairs of semilunar valves.

B—Blood allowed to pass in one direction only.

C—Back flow of blood being prevented by valves.

by a relaxation of its muscular walls (**diastole**). The heart beat is not simultaneous for the entire heart, but originates at one point and spreads as a wave of contraction (**Fig. 50**). A heart preparation in an isotonic salt solution goes on beating even after cutting away the vessels. This can be seen in a heart which is several inches long, as in *Limulus* (Arachnida). Here the heart beat originates in a compact **cardiac ganglion** which lies on its dorsal median part. The heart beat is also moderated by a pair of lateral nerves from the brain and from abdominal ganglia. Stimulation of the abdominal ganglia accelerates the heart beat, while stimulation of brain or lateral nerves slows its down. This is called an **antagonistic mechanism** which has been demonstrated in invertebrate as well as vertebrate hearts. The vertebrate medulla

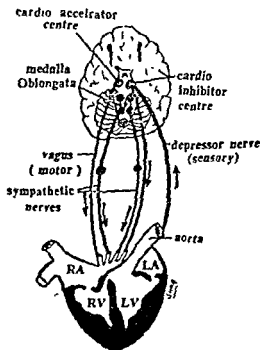


Fig. 51. Neurogenic antagonistic mechanism for control of heart-beat. (Arrows indicate the direction of nervous impulse).

has both a cardiac accelerator centre and a cardiac inhibitory centre (**Fig. 51**).

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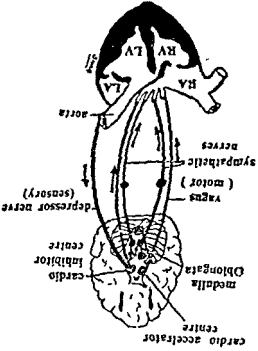


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has both a cardiac accelerator centre and a cardiac inhibitory centre (Fig. 51).

In *Sepia* (Cephalopoda) the vena cava splits into two afferent branches, each of which leads into a contractile **branchial heart**; the blood being collected from the gills and poured by efferent vessels into a **systemic heart**. The beats of the two branchial hearts and systemic hearts are synchronised by a nervous mechanism. However, it is surprising that in the embryo the heart starts to beat before it is supplied by nerve fibres. It appears, therefore that the heart muscle itself is the initial pace maker in the invertebrates, and is latter superceded by a nervous one.

In vertebrates also the heart begins to beat before any nerve ganglia develop e. g. at ten somite stage in chick; while in rat embryos contraction starts even before the heart primordia fuse; and extirpated parts of the heart (in normal Ringer's solution) beat at different rates. The controversy between **myogenic (muscular)** and **neurogenic (nervous)** theories of heart beat, is therefore futile, in as much as both are present in invertebrates as well vertebrates.

Thus it can be safely concluded that the origin of the heart beat is myogenic; while it is superceded by the neurogenic mechanism in most higher animals.

Control of Heart Beat (Conductile Mechanism)

The origin of the control of heart beat has been discussed above. However, the exact **conductile mechanism** as obtains in higher vertebrates and specially mammals, is given below.

The control outside the heart is through : (i) the sympathetic thoraco-lumbar fibres called the **accelerator nerves**; (ii) vagus nerve which carries parasympathetic fibres with it. Stimulation of the accelerator nerve speeds up the heart beats while stimulation of the vagus retards it. But if both these nerves are cut, the heart still continues to beat normally. This is because the heart has within itself two neuro-muscular centres which are partly nervous and partly muscular.

The first such centre is called the **sinu-auricular (atrial) node**, (**S. A. node**) or **node of Tawara**. It lies embedded in the

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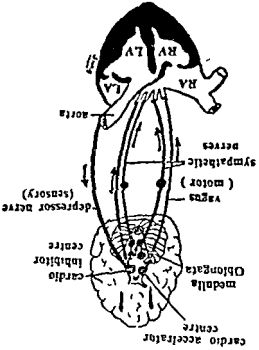


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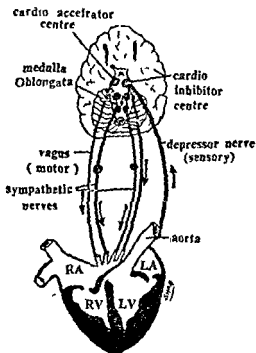


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The first such centre is called the **sinu-auricular (atrial) node**, (**S. A. node**) or **node of Tawara**. It lies embedded in the

wall of the right auricle in mammals, at the junction of the superior vena cavae. The second centre called the **atrio (auriculo)-ventricular node or (A.V. node)**, lies in the septum between the right auricle and the right ventricle (Fig. 50). Its fibres are continued into the inter-ventricular septum, as the **atrio ventricular bundle (bundle of His)** extending upto the bases of the papillary muscles of the ventricle. Thus the S. A. and the A. V. node, together with the bundle of His co-operate to control the rhythm of the heart beat even in absence of nervous stimulation or control.

The **cardiac impulse** which sweeps over the heart, effecting the **cardiac cycle**, originates in the S. A. node, which is thus known as the **pace-maker of the heart**, (in the heart of lower vertebrates, *e. g.* fishes and amphibia, the heart beat originates in the sinus venosus). From the S. A. node the cardiac impulse is conducted to the A. V. node, from which the wave spreads along the **bundle of His**, in its right and left branches (right and left ventricles), to end finally in branching fibres (Purkinjee fibres) in the ventricular musculature.

The Blood (Fig. 52).

The blood is the circulating body fluid in all higher animals except for some invertebrates, *e.g.* Hirudinea Arthropoda, Echinodermata *etc.*). Blood is a tissue, containing different types of cells capable of metabolic changes. As already explained in the Chapter on Respiration, the blood contains four types of respiratory pigments either in the fluid matrix (plasma) or carried by the blood cells (**haemoglobin, haemocyanin, haemerythrin and chlorocruorin**). Although haemoglobin is found in some scattered groups of invertebrates it is the only respiratory pigment of all vertebrate bloods.

Vertebrate blood is a cell-containing fluid, transporting oxygen, food materials, salts, wastes, metabolic wastes and hormones, as and when necessary. It provides a means for maintaining osmotic pressure of tissues and cells and a constant internal environment. In addition it is a medium for mobilising defences against

injury and disease. Blood is a short-lived tissue, all the cells being completely replaced great many times during an individuals life

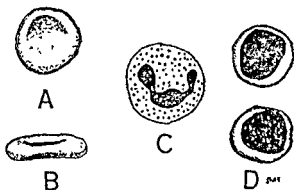


Fig. 52. Blood cells in Man—
 A—Erythrocyte (Surface view)
 B—Erythrocyte (side view)
 C—Granulocyte
 D—Lymphocyte

time. In man it forms 7.8% of the body weight. The blood is composed of the fluid **plasma** constituting 55% of the total and the **blood cells**, 45%.

The plasma or fluid matrix

Blood Plasma is a veritable gold mine of proteins. These are of three types: (i) **albumins**; (ii) **globulins**; (iii) **fibrinogens**. The total **dissolved salts** (about 1% in plasma) consist of chlorides, bicarbonates, sulphates and phosphates of sodium and potassium. Due to these salts the pH of the blood is slightly alkaline (pH between 7.3 and 7.5 in man). Glucose, fats, aminoacids and lecithin are other substances normally present in the plasma. Besides these urea is always transported in blood, dissolved in plasma. Finally, the endocrine glands pour hormones into the blood, which are carried by the plasma to target organ. Minute amounts of anti-bodies and anti-toxins for the neutralization of foreign bodies and poisons are also present in plasma.

The Blood cells or corpuscles: The blood corpuscles are of three kinds (i) **erythrocytes** or red blood corpuscles (R. B. Cs.);

(ii) **leucocytes** or white blood corpuscles (W. B. Cs.), and (iii) the **thrombocytes** or blood platelets. All the blood cells are unattached and float freely in the plasma. It is surprising that none of these cells divide or multiply in the blood.

The erythrocytes in mammals are enucleated (without nucleus), circular, biconvex discs (except in camel where they are nucleated and oblong). They are far more numerous than the leucocytes, and are formed from erythroblasts in the spleen in young and in the red bone marrow at all ages. R. B. Cs. number from four to five million in each cubic millimeter of blood; while the W.B.Cs are only about 8,000 per cubic millimeter of blood in man. The average life span of an R. B. Cs. in man (as counted by geiger counter after injecting radioactive chromium) turns out to be only 65 days instead of 120 days previously estimated.

The leucocytes in mammals are of two main types; (i) **granulocytes** (about 65%) having a beaded nucleus and granular cytoplasm; (ii) **agranulocytes** or **lymphocytes** (about 35%) having a large nucleus and produced in the lymph nodes. The life span of granulocytes ranges from 4-12 days and agranulocytes about a few hours only.

The **thrombocytes** are small cell fragments without nuclei, floating in the plasma, numbering from two to four hundred thousand in each cubic millimeter of blood.

BLOOD COMPONENTS AND THEIR FUNCTIONS

Plasma: (1) The water component maintains blood volume and blood pressure; forms the bulk of the lymph; provides transport for all constituents in blood including hormones.

(2) The mineral ions maintain osmotic balance, pH balance (slightly alkaline), and proper functioning of tissues.

(3) Plasma proteins (fibrinogen, prothrombin, albumins, globulins and enzymes) help in blood-clotting, maintaining O. P. and pH and most important of all, form the basis for blood types and antibodies.

(4) Glucose is supplied to tissues for ready oxidation and energy production.

(5) Urea, CO_2 and O_2 , absorbed foods, vitamins *etc.* are transported to and from cells of tissues.

Erythrocytes: R. B. Cs. consist of a spongy protein material called **stroma** surrounded by a cell membrane. The composition of R. B. Cs. solids approximates: Haemoglobin—29%; Other proteins—upto 1%; Fats—1%; Other Organic substances—0.2%; Inorganic substances—0.7%; Total solids—about 32%

Haemoglobin is packed in the interstices of the stroma. Essentially haemoglobin consist of a large protein molecule called **globin**, which is united with four molecules of a compound called **porphyrin** (Fig. 53). Each porphyrin molecule includes four

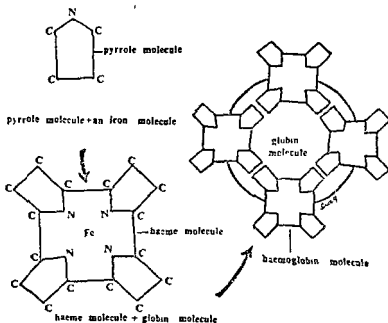


Fig. 53. Formation and composition of a Haemoglobin molecule.
(After D'Amour)

pyrrole groups with differing side chains which produce the various kinds of porphyrins. A molecule of porphyrin combines with an

Leukemia (blood cancer) produced in man is caused by a sudden rise of the W. B. C. count. This may be caused by exposure of body to gamma rays, X rays or radioactive fall out from nuclear fission (A bomb, H. bomb). Besides there can be several other reasons, unknown yet. In granulocyte leukemia, the granulocyte producing bone marrow is affected, while in lymphocytic leukemia, the lymphocytes inhabiting lymph nodes become over active. In the former the granulocyte count may rise as high as 500,000 per cubic mm, and in latter the lymphocyte count may be as high as 200,000 per cubic mm. This abnormal over-production of W. B. Cs. uses up much of the available food in blood. With this over-production of white cell the R. B. C. count falls sharply resulting in severe anemia and consequent death.

Thrombocytes or Platelets

These small blood cells are numerous about 200,000 to 300,000 per cubic mm of blood. They are formed from large cells in bone marrow, called **megakaryocytes**. Thrombocytes have a life span of only about 4 days. The function of these platelets is double: (i) they are involved in blood coagulation; and (ii) they plaster up small injury holes in the capillary walls. They are finally destroyed in the spleen.

BLOOD VOLUME AND BLOOD PRESSURE

Blood volume and blood pressures in animals differ widely. The blood volume as a percentage of body weight is highest in crustacea (25-37% in cray fishes); in cockroach it is 10.5%; in fresh water mussel only 9%. In the vertebrates the percentage ratio falls to 8.7% in dogfish and 8% in frog, dog (approximately 5 liters). In the rabbit it is only 6.5% while in the fish it is the lowest, being 3%. Blood pressure (systolic/diastolic pressures). In man it is 120/80 mm Hg. (systolic pressure/diastolic pressure); in the frog it is 16/12 mm Hg. while in the rayfish it is 16/7.4 mm Hg. However, in the vertebrates blood pressure is calculated as mean pressure during systole and diastole. In an active earthworm it is 12/8 mm Hg. In water mussel only 4.4, 9.6 in cray fishes; in the dogfish it is 12/8 mm Hg.

dragonfly nymph it is as high as 33 mm Hg in the abdominal haemocoel.

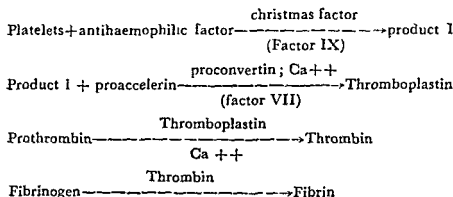
We have stated that the normal blood pressure of man is 120/80 mm Hg. However, these values vary considerably due to age, disease, puberty *etc.* In infants the B. P. is about 90/60; in puberty 110/70; and a fifty years old man has 110-135/75-85 compared to the normal 120/80 of adults. There is also a sexual variation in B. P., that of the female being somewhat lower than the male. Again, during sleep the B. P. falls by 20 to 30 mm Hg.

In obese (fat) individuals the B. P. is always higher than normal persons and therefore, they usually suffer from hypertension. It should also be noted that during exercise, specially violent exercise, the systolic pressure may reach 180-200 mm Hg. High Blood Pressure can be effectively reduced by the use of Reserpine (a drug obtained from an Indian herb *Rauwolfia*—'choota chand') which also cures hypertension temporarily. (About 70% of the people suffering from hypertension due from heart failure). On the other hand, the low pressure suffers from traumatic shock in the hustle and bustle of the world of today; and some may even die of low B. P. heart failure long after an accident.

BLOOD COAGULATION

The most primitive arrangement for haemostasis depends on the contractility of body musculature and blood vessels, which is common in the soft bodied invertebrates. However, such a device would fail in hard bodied invertebrates, such as arthropods, and echinoderms. In such animals, the vascular fluid contains cellular elements and special jellying proteins which form plugs at the time of injury. In some of these hard bodied invertebrates, cell agglutination is followed by plasmodium formation, with fusion of protoplasm of several cells. This results in the production of fibrous protein material for entangling other cells and this increases the size and strength of the coagulum or plug. The invertebrate fibrous material is called cell fibrin, but is not biochemically similar to the fibrin of vertebrate blood.

In the vertebrate blood, clots are composed of tangled protein fibres which develop from a plasma protein called **fibrinogen**. The conversion of fibrinogen into fibre—like **fibrin** is an enzymatic reaction initiated by chemicals released from injured cells. Among the lower vertebrates (fishes, amphibia and reptilia) the thromboplastic activity, responsible for conversion of fibrinogen into fibrin, is almost completely contained in cells and released only when they reapture. However, in the mammals the thromboplastic mechanism is controlled by several factors found in the plasma. Recent researches, have demonstrated over a dozen distinct factors in the plasma responsible for blood coagulation. In mammals fibrin formation is usually as follows:—



Therefore, to start the clotting of blood the one factor necessary is the enzyme thromboplastin, which activates prothrombin of the plasma that is the precursor of thrombin. The action of thromboplastin requires the presence of calcium ions, which are normally present in blood plasma. Blood platelets (about half million/cu. mm of blood in man) are extremely sensitive to contact with damaged tissues, when they disintegrate rapidly to release thromboplastin in blood.

It has been stated that the thrombocytes of fishes and amphibia provide all of the thromboplastic factors shown above. Reptiles and birds are also deficient in plasma thromboplastic components, and they rely more on vasoconstriction and **tissue thromboplastin**.

Several **anticoagulants** are present in mammalian plasma to provide safeguards against clotting during circulation (leading to **thrombosis** of heart, brain or other vital organs). **Heparin**, a muco-polysaccharide, produced by the liver, is one powerful anticoagulant, preventing intravascular clots. Another anticoagulant **hirudin** is produced by the leech. The anticoagulants of the saliva of blood-sucking insects prevent blood clotting at the time of sucking of blood from hosts. Similarly the venom of the viper contains a powerful proteolytic enzyme which causes **haemolysis** (breaking of R. B. C. and running out of haemoglobin into plasma), when the snake bites man or other mammals.

Prothrombin production requires Vitamin K for its synthesis; in its absence prothrombin is not formed at all, and the blood does not coagulate. This vitamin K is normally produced by bacteria in the intestine of man and other mammals. Thus the destruction of intestinal flora by powerful broad spectrum antibiotics can lead to fatal bleeding. One compound **dicoumarol**, which is formed in spoiled clover hay (alfa alfa), causes internal bleeding in cattle and live-stock if they eat it. This is thus used in rat poisons, since some rats have an uncanny ability to avoid poisoned baits.

This disease in man called (**HAEMOPHILIA**), which is congenital and inherited according to Mendel's Genetic laws, is caused by the failure of the blood to clot, due to patient's platelets failing to rupture and release prothrombin. It is now believed that the failure of the platelets to rupture is caused by the absence of the **ANTI-HAEMOPHILIC FACTOR (A H F)** which is essential for the rupture of platelets. As a matter of fact, a substance called **ANTI-HAMOPHILIC GLOBULIN (A H G)** prepared from the blood of cattle is now being used in the treatment of haemophilia. Haemophilia occurs only in males, but is transmitted genetically through the mother to her sons. The gene for haemophilia, carried on the X chromosome is recessive in the female (where XX chromosomes are present). The chromosome in the male does not carry the gene dominant for haemophilia. Therefore this disease is not being dominated by another gene (as only one X chromosome is present in male). The characteristic of haemophilia is that it is a recessive trait.

and the Czars carried this character which was expressed in some of their male offspring, and as they kept a careful genealogical chart it was possible to trace the mode of transmission as a Mendelian recessive character).

BLOOD GROUPS

Karl Landsteiner (N. L.) was the first man to discover the types or groups of human blood in early 20th century. However, the connection between fatal blood transfusions and blood groups was established in practice much later. After examining the blood of a large number of persons, he showed that transfusion agglutination (clumping) of blood was caused by two kinds of 'adhesives' (called **agglutinogens**) clumping the R. B. Cs. together; one of which he called **A** and the other **B**. Some persons had both the types of such binding substances and were thus **AB**; whereas the fourth type were those with no agglutinin at all, and thus, belonged to Zero group. Landsteiner found that the specific agglutinogens bind R. B. Cs. in presence of certain specific substances called **agglutinins** in the plasma.

By statistical analysis it has been calculated that:—

(1) **Type O** (47% of all people) have agglutinogens in their R. B. Cs. but have **a** and **b** agglutinins in their plasma.

(2) **Type A** (41%) have **A** agglutinin in R. B. Cs. and **B** agglutinins in plasma.

(3) **Type B** (9%) have **B** agglutinin in R. B. Cs.; and **a** agglutinin.

(4) **Type AB** (3%) have **A** and **B** agglutinogens but no agglutinins.

As stated, above people with agglutinin **A** in R. B. Cs. do not have the agglutinin **a**, presence of which would lead to the clumping together of R. B. Cs. in the blood. However, the R. B. Cs. contain the agglutinin **b**. Therefore, if blood from a person belonging to group **B** is transfused into the body of an **A** group person, the R. B. Cs. of the **B** blood will clump. It is therefore essential to know the agglutinin present in the recipients blood

during a blood transfusion, which is normally determined by addition of anti-sera (Fig. 55). If such a precaution is not taken,

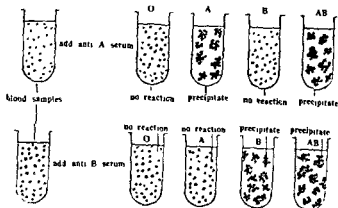


Fig. 55. Blood group determination by the addition of anti-sera.

the result will be fatal. The following table gives the compatibility (matching) of the blood types.

Donor	Recipient			
	Group O (agglutino- gen nil aggluti- nin ab)	Group A (agglutino- gen A aggluti- nin b)	Group B (agglutino- gen B agglu- tinin a)	Group AB (agglutino- gen AB agglu- tinin nil)
Type O	No clumping	No clumping	No clumping	No clumping
Type A	clumping	No clumping	clumping	No clumping
Type B	clumping	clumping	No clumping	No clumping
Type AB	clumping	clumping	clumping	No clumping

As is evident from the above table, blood from type O person can be transfused into any type of recipient; type O is therefore known as **universal donor**. On the other hand type AB can receive blood from any type of donor; type AB is therefore called the **universal recipient**.

Rh factor

Even after matching the regular blood groups (O, A, B, AB) an occasional transfusion still resulted in fatal blood clotting for the recipient. Landsteiner tried to find the cause of this abnormal phenomenon. He found that R. B. Cs. of **Macacus rhesus** (oriental monkey) when injected into a rabbit cause the rabbit to produce a substance which clumps R. B. Cs. of the monkey. This he called a straight antigen-antibody reaction (antigen being the monkey's blood and the antibody produced by the rabbit's plasma).

It was found that by adding the some rabbit plasma to a suspension of human R. B. Cs. the R. B. Cs. of about 85% people tested clumped; while in 15% blood did not agglutinate. The 85% formed the **Rh positive** group as their R. B. Cs. behaved as did the monkey's. The other 15% denote the **Rh negative** group. Therefore, if to a **Rh negative** person, blood is transfused from an **Rh positive** person (even if the blood group is compatible), the blood acts as a foreign protein antigen causing clumping.

If an **Rh negative** woman marries an **Rh positive** man and conceives an **Rh positive** baby, then the **Rh positive** cells of the unborn baby cause the mother to produce antibodies against them. These antibodies go on being concentrated in the mother's blood with each subsequent conception (taking that only **Rh positive** babies are conceived every time) until they become so strong as to be fatal for the now developing baby. In such cases to save the baby the entire blood must be replaced by **Rh negative** blood, after birth.

Rh positive factor is dominant to **Rh negative** as regards its inheritance.

Inheritance of Blood Types (Fig. 56): Blood types are hereditary. **A** and **B** are equally dominant to each other. The presence of **A** or **B** is also dominant against their absence (**O**). Thus, a person may be either **AA** or **BB** (homozygous dominant); **AO** or **BO** (heterozygous but still belonging to type **A** or **B**). The

offspring of parents both belonging to type A (AA or AO) might belong to either type A or O. If type A (AA, AO) mates with

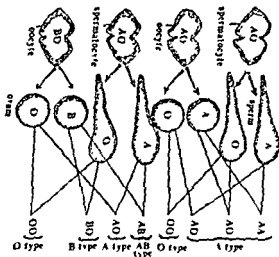


Fig. 56 Diagrammatic representation of inheritance of blood groups

(The presence of A or B is dominant over their absence in O, while towards each other they are equally dominant).

type B (BB, BO) the offspring may belong to any of the four groups. On the other hand, if gene A should meet gene B, such an individual would be AB, since A and B are equidominant.

Genetic blood tests are sometimes carried out to establish paternity. It may be stated that such genetic blood tests can only show that Mr. A might or might not be the father and not that he positively is the father (also Supreme Court ruling). For example if Mrs. A (mother) is type O, and her baby type A, and Mr. A ("father") turns out to be type O, he cannot possibly be responsible for the child!

LYMPHATIC SYSTEM

The lymphatic system consists of (i) **lymphatic capillaries**; (ii) **lymphatic vessels**; (iii) **lymphatic nodes**; and (iv) **lymphatic fluid or lymph**. The lymphatic capillaries are extremely thin-

walled vessels which send their ramifications into all the tissues of the body.

The lymphatic vessels formed by union of lymph capillaries become larger as the smaller ones unite. At many such junctions lymph nodes (Fig. 57), are formed which are supplied by an

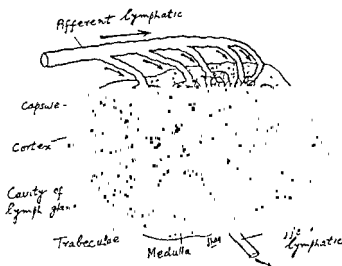


Fig. 57. The structure of a lymph node (After Das)

afferent lymphatic and drained by an efferent lymphatic vessel. Each lymph node, consisting of a cortex, medulla, and projecting trabeculae, contains lymphoid tissue and lymph spaces, which produce lymphocytes. Lymph is circulated by muscular contractions and movements of the body. Finally in mammals all the lymph from the lower parts of the body enters a large vein (left external jugular) through a lymph vessel called **thoracic duct**. Thus, the lymph is returned into the blood, where from it originally came.

Lymph (the fluid of the lymphatic system) transudes from blood plasma through any membrane which is partly permeable to proteins. It forms sort of a secondary circulation to bathe all the cells of the body. The electrolytic and crystalloid content of **lymph** is approximately the same as that of plasma, but the protein content is only half of plasma.

The osmotic pressure (OP) of lymph is lower than that of plasma (*i. e.* it is hypotonic to plasma). The protein content of lymph varies according to the part of the body from which it is collected (*e. g.* lymph from liver is rich in protein). It also contains fibrinogen, since it clots on standing. Again, the lacteals of the intestine after a meal contain high percentage of emulsified fat which gives it a milky colour.

The cellular contents of the lymph are mainly **lymphocytes**, which are produced in the lymph nodes. These nodes swell up when the lymphocytes fight an infection *i. e.* when a wound septic or after an inoculation.

Functions of lymph: (1) transport of nutrients; (2) production of lymphocytes; (3) destruction of bacteria and filtration of foreign bodies; (4) production of antibodies; (5) lubrication of joints (synovial fluid).

Chapter VI

EXCRETION AND OSMOREGULATION

EXCRETION (EXCRETORY SYSTEM)

Excretion originated in animals due to the necessity of removal of metabolic nitrogenous materials formed during activity of organs in the body. Excretion involves the triple mechanism of filtration reabsorption and active excretion of metabolic wastes. Filtration were the primary prerequisites for balance of water and salts in the body (explained later); and excretion was combined physiologically with osmoregulation at an early stage of life, due to the ease with which nitrogenous waste products could be removed from the organism, in solution.

EXCRETION IN INVERBTERATES

The simplest type of excretion is found in the **protozoa**, where the contractile vacuole (which is essentially an osmoregulatory organ) excretes the waste products. *Glaucoma* and *Didinium* excrete only ammonia; *Amoeba* forms ammonia and uric acid; *Paramecium Spirostomum Euglena Conchophthirius*, excrete both ammonia and urea; **Colpidium** ordinarily produces ammonia, but in a thick culture it also forms urea. These products are concentrated in the contractile vacuole and expelled out of the organism along with excess water (Fig. 58). However it has been demonstrated now that elimination of ammonia and urea from the protozoan body is to a large extent through the thin surface membrane. For example, if the concentration of urea in a culture of *Paramecium* be back-calculated to the rate of elimination of water by vacuoles alone, then the concentration in vacuoles should be one part of

urea in 2,000-3,000 parts of water. But by injection of xanthydrol into the vacuoles (xanthydrol is sensitive to one part of urea in 12 thousand parts of water) the results are negative, indicating

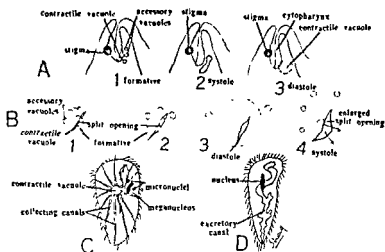


Fig. 58 Osmoregulation, osmoregulation in some Protozoa.

of contractile

C—Collecting canals opening into contractile vacuole in *Frontonia*.

D—Permanent excretory canal in *Protoopalina*.

that not even one part of urea in 12 thousand parts of water is present in the contractile vacuule. Where did the higher concentration of urea in the culture come from. Therefore, it can be safely concluded that waste products diffuse out through the cell wall.

Besides the waste products eliminated in solution, certain insoluble products are deposited as crystals, e. g. *Paramecium* has acid calcium phosphate granules stored in the cytoplasm. Again, the shells of *Foraminifera* and *Radiolaria* are excreted CaCO_3 , strontium sulphate and silica, or even nitrogenous compounds. This is further confirmed by the protoplasm lying outside the shell in *Foraminifera*, as in *Polystomella*. The peculiar Muller, vesicles and concretment vacuoles seen in some Protozoa *Loxdes*, *Blepharoporthium* throw out solid concretions, (Fig. 59).

In the **coelenterates**, uric acid has been demonstrated in the sea-anemone *Anemonia*, and urea in other sea-anemones. No specialized excretory organs are present and thus waste products escape

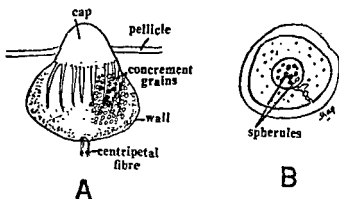


Fig. 59. Excretion.

A—Concrement vacuole with concretions in the protozoan *Blepharoprosthium*

B—Muller's vesicle in the protozoan *Loxodes* containing concrement spherules.

through the general surface. If the Protozoan excretion theory of skeletons be applied to coelenterates, the huge coral rocks and islands are nothing but excretory products of tiny hydrozoa and actinozoa.

The **platyhelminthes** have evolved definite excretory organs called **protonephridia** containing the characteristic **flame cells** (solenocytes). Although the chemical composition of excretory products is incompletely known, there is evidence to show that the chief excretory product is ammonia (*Planaria*, *Fasciola*, *Taenia*), whereas nematodes ordinarily excrete $\frac{1}{3}$ rd as ammonia and the rest as amino-acids and peptides. It may be mentioned here that the protonephridia are osmoregulatory as well. Cercariae (of trematodes) have a pulsating terminal excretory vesicle, the rate of which slows down in salt solutions and stops in sea water.

Annelids have ammonia as the chief excretory product e. g. the polychaetes and the leeches. But in earthworms ammonia is only 20% ; 40% ; being urea and the rest amino-acids and purines. However, *Pheretima posthuma*, the Indian Earthworm has ammonia

and urea about 50-50, with traces of creatinine. The nephridial system of the annelids as a segmentally paired organ but in the earthworms it is a most elaborate system consisting of thousands of exonephric and enteronephric nephridia. These expell the waste products outside the body and inside the gut respectively. Besides, in the earthworms uric acid crystals are ingested by the amoebocytes of the coelomic fluid and after getting loaded they escape outside with the coelomic fluid. The gephyrian annelids store their nitrogenous wastes as **brown bodies** in the coelom. A physiological complication is the formation of nephromixium, in the polychaeta, where the physiology of reproduction and excretion are combined, and can be called the earliest urinogenital system.

Little work has been done on excretion of arthropods except a few insects. **Crustacea** generally appear to excrete ammonia and amin-compounds as excretory products. Nitrogenous wastes are expelled by **antennary glands** with bladder (**green glands**) of decapods (Fig. 60), which are also osmoregulatory in function. In

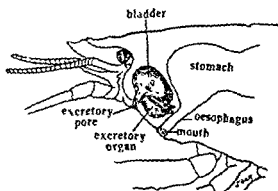


Fig. 60. Green gland with bladder as excretory organ in Crustacea.

the crab *Cancer*, the excreted substances are purines, which however are absent in the crayfish. Again, like the skeleton of protozoa and coelenterata, the exoskeleton of chitin and CaCO_3 can be considered as products of excretion.

In **Insects** uric acid is the normal nitrogenous product, but traces of urea, allantion, ammonia and amino compounds have been

demonstrated severally in clothes moth, dipteran maggots and dityscid beetles. Some Orthoptera convert allantoin into allantoinic acid.

The standard excretory organs of insects (*e. g. Rhodinus*) are the **Malpighian tubules** (Fig. 61), excreting both nitrogenous wastes

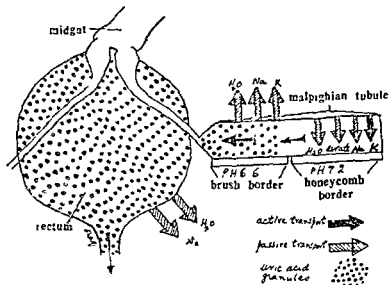


Fig. 61. Diagrammatic illustration of the Malpighian tubule excretion in *Rhodinus* (Insecta).
(After Stobbs and Shaw 1964)

and carbon dioxide. Secretion of potassium or sodium urates is common in the upper part of the Malpighian tubule; while its lower part reabsorbs water and some ions, as well as precipitates free uric acid (Fig. 62). The contents are excreted in most insects by peristaltic action of the tubules.

Subsidiary excretory organs may be present, such as fat bodies, storing uric acid. For example *Colembella* have no Malpighian tubules and wastes are stored throughout life in fat bodies. The labial glands of some insects; and the **nephrocytes** (chains of cells along the heart or oesophagus) also store wastes. Calcium carbonate may also be deposited and excreted at ecdysis, called **ecdysial excretion**. Similarly the white pigment in

the wings of butterflies consists of uric acid formed during larval life, stored in the fat bodies and transferred to the wings

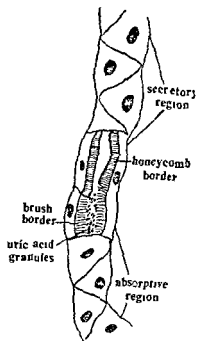


Fig. 62. Functions of parts of the Malpighian tubule of the insect *Rhodnius*.
(After Wigglesworth)

at emergence of imago. The **coxal glands** of spiders eliminate urates.

Mollusca excrete ammonia and amino compounds; but urea, uric acid and purines have also been detected. Sixty percent of fresh water mussel excretion is ammonia, but the peculiar organ of *Bojanus* contains concretions of magnesium phosphate. The **kidneys** of mollusca are responsible for only part of the excretion, subsidiary excretion being by gills, mantle or even general body surface. Terrestrial slugs excrete chiefly urea; while the urine of marine cephalopods (octopus, cuttle fish, etc.) contains ammonia, trimethylamine, amino compounds and small quantities of urea and purines.

In the **Echinoderms** the water vascular system contains small amounts of ammonia, urea, uric and amino compounds. These are excreted out of the water vascular system with general flow of sea water.

EXCRETION IN VERTEBRATES

The Vertebrate Kidney: We have seen that excretion in invertebrates is carried out in the main by **nephridia**, which are present in *Platyhelminthes*, *Rotifera*, *Annelida* and *Mollusca*. Amongst the chordates *Amphioxus* (*Branchiostoma*) also has homologous nephridia. How and when nephridia evolved or were replaced by the vertebrate kidney is not clear; but the kidney has occupied the most important role in excretion and osmoregulation in all the vertebrate series. It eliminates water, ammonia, urea, uric acid, sodium chloride, sulphuric acid, and phosphates.

Although the **kidney** is called a pronephros, mesonephros or metanephros, according to the structure and stage of evolution, it is always built on the same general plan. Essentially it consists of a mass of **coelomoducts** (remaining one of the nephromixium of the polychaets which open into a single longitudinal **collecting duct**. The details of the highest evolved **nephron** or excretory unit can be seen in the mammalian kidney, in which all the coelomoducts have lost their openings into the coelom and start as a blind **Bowman's capsule**. In the cavity of Bowman's capsule lies a bundle of blood capillares from the renal artery (afferent and efferent arterioles) forming the **glomerulus** (Fig. 63). The main segments of the nephron in mammals are:—

- (1) A double-walled **Bowman's capsule** embracing a **glomerulus** and together forming a **Malpighian capsule**;
- (2) a short and thin **neck segment**;
- (3) a stout **convoluted proximal tubule** in the cortex;
- (4) **descending limb of Henle** passing into medulla becoming thinner and bending sharply outwards;

(5) the loop of Henle, the distal arm of which runs towards the cortex, where it forms the ascending limb of Henle, which passes into the coils of the

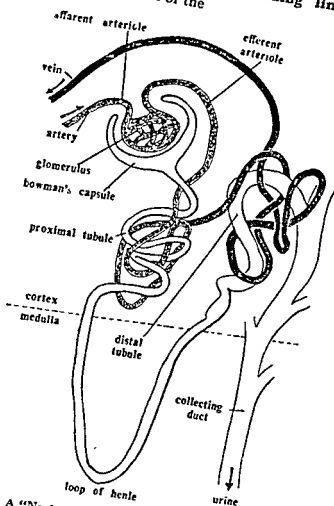


Fig. 63. A "Nephron" or excretory unit in mammals, showing glomerulus, Bowman's capsule, loop of Henle, tubule and capillary network.

(6) **distal convoluted tubule.** It is thick and intertwines the proximal tubule of its own nephron and distal convoluted tubules of other nephrons.

(7) A short **junctional tubule** connects the distal convoluted tubule with a **collecting tubule** which passes from cortex into

medulla. A number of collecting tubules join and open into the pelvis of the kidney.

It was **Bowman** (1842) who deduced from the construction of the Malpighian body, that water is withdrawn from blood in the glomerulus, and is drained into the Bowman's capsule (named after him). However, he thought that all other elements of urine were secreted by the kidney tubules. **Ludwig** (1866) postulated that all the constituents of urine were filtered by the glomerulus and urine was only concentrated (through passive reabsorption of water) by the kidney tubules.

Cushney (1926) accepted Ludwig's filtration theory but contended that passive diffusion could not explain reabsorption in the tubules. He believed that excretion was a vital phenomenon and not a mere physical process alone. **Hyman** established that there was an effective **filtration pressure** in the glomerulus, which could only be performed by live cells.

Urine Formation

The working of the nephron involves three processes: (i) a physical process of **filtration** of a portion of the blood plasma water with its dissolved solutes; (ii) **selective reabsorption** of some substances; and (iii) **active secretion** of certain substances.

1. Filtration

It has been shown that the pressure in the capillaries of glomerulus is higher than that of any other capillary in the body, being about 60 mm (30 mm in other capillaries). This high pressure is sufficient to force blood fluid through the efferent vessels of the glomeruli. On account of this high pressure blood fluid is driven through the walls of the thin capillaries. The **capsular fluid formed** by filtration contains all the components of blood minus the plasma proteins, lipids (fats), and cellular elements.

There is however, an O. P. factor which must also be considered, since blood cells and blood proteins cannot pass through the glomerular capillaries, and the Bowman's filtrate contains

only water dissolved salts, urea, glucose *etc.* Thus the O. P. of the blood is always higher than the filtrate in Bowman's capsule, which acts as a force restraining the further flow of fluid into the capsule. Therefore, the first step in urine formation in vertebrates consists simply of the filtering of blood as it passes through the capillaries of glomerulus into the Bowman's capsule. The rest of the blood (after filtration) continues to flow through efferent arteriols in to the capillaries surrounding the tubules, where most of the fluid is reabsorbed and returned to the blood.

There is definite recent evidence that the Malpighian bodies act as ultra-filters, which separate water, along with certain other compounds from the plasma; the filtering membrane being permeable to molecular weights smaller than 70,000. Gelatin (m w.—35,000) and even haemoglobin (68,000) may be passed out while the normal serum proteins of higher molecular weights are retained in blood.

2. Active Reabsorption

The reabsorbed substances from the glomerular filtrate are those which are important to the body, such as glucose, amino-acids salts and water. They are called **threshold substances**, because for each of these, there is a threshold, beyond which the kidney tubules cannot reabsorb them. The urine passed out of the kidney tubules is much more concentrated than the glomerular filtrate, on account of active reabsorption

Below are given some threshold substances in order of their reabsorption by kidney tubules :

glucose	}	almost completely reabsorbed
sodium		
chlorides		
potassium		
<hr/>		
ammonia	Threshold	
phosphates		
sulphates		
Foreign bodies		
urea		
water		

Micturation

The act of emptying/urinary bladder is called **micturation**. The urine from the renal pelvis is conveyed by the muscular ureter (exhibiting **peristaltic waves**) into the urinary bladder. The ureters have an oblique entrance into the bladder which act as a valve and prevent reflux of urine back into the ureters, when bladder is full.

When the bladder is full, the pressure stimulates the pressure receptors in the bladder wall, which cause reflex contraction of the bladder, with simultaneous relaxation of the sphincter around the urethral orifice of the bladder. Ordinarily micturation is a forcible reflex, expulsion of urine through the urethra. But this reflex is controllable by most mammals, *e. g.* the dogs at the tree and man in the bathroom.

Functions of the Kidneys

The main functions of the kidneys are summarised as under:—

(1) **Excretion of Waste Catabolic Products and Toxic Substances** (described earlier).

(2) **Regulation of the Water Content of the Body** (explained later).

(3) **Regulation of the Osmotic Pressure of Body.** Osmotic pressure is regulated by: (i) keeping constant the electrolyte content of the body (achieved by selective reabsorption of the filtered sodium and almost all potassium); (ii) by retention of certain vital substances such as glucose, amino acids phosphates, bicarbonates and proteins.

(4) **Maintenance of the Normal Acid Base Equilibrium of the Blood.** The pH of blood in man is maintained at 7.35 *i. e.* slightly alkaline. This is due also to the ability of kidneys to actively secrete Hydrogen ions as ammonia (Fig. 64).

All **mammals**, including the egg/laying monotremes are **ureotelic**; their urine contains upto 87% of the total N_2 excreted

as urea. In land mammals, since there is need for conservation of water, the urea in the kidney tubules may be concentrated as much as hundred times by the reabsorption of water.

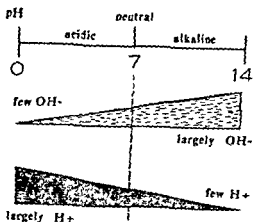


Fig. 64. Diagrammatic representation of pH scale.

In desert animals there is active tubular secretion of urea on account of low water intake. On the other hand ruminants use up the excretory urea as the ultimate protein source of the body when kept on low protein diet. Similarly camel and sheep reduce urea excretion twenty fold under the same conditions. Therefore ureotelic animals are not highly dependent on water supply as do the ammoniotelic animals.

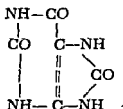
Uricotelic animals are those adapted to dry environment such as the earthworm *Pheretima*, and insects amongst invertebrates, which excrete Nitrogen in the form of uric acid. A surprising amount of 91% uric acid constitutes the highest percentage of N_2 excretion by the insect *Rhodinus*. Amongst vertebrates the reptiles and the birds are uricotelic animals. Water conservation is as important for lizards and snakes as for the birds; in addition their hard shelled eggs retain the embryonic nitrogenous excretion in the form of inoeous uric acid. In the desert lizard *Phrynosoma* (the horned toad) the urine is a solid ball of uric acid. Similarly, in birds the urine is a semi-solid mass of uric acid crystals (which may be seen as the white portion

of the faces of the fowl where the percentage of N_2 excretion in the form of uric acid is 87%).

The other compounds of N_2 excretion are guanine, creatinine, trimethyl amine and allantoin. *Spiders* excrete N_2 predominately as guanine, the Malpighian tubules and the cloacal sacs elaborating it. Creatinine is high in cat and the camel (10%), followed by the bat (8.5%) and man (3.6%).

Nitrogen Excretory Products

In the forms of nitrogen excreted, the chief ones are ammonia (NH_3), urea $CO(NH_2)_2$ and urea acid



Ammonia, urea and uric acid excreting animals are called **ammonotelic**, **ureotelic** and **uricotelic** respectively.

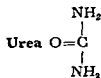
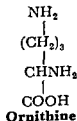
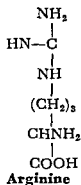
Ammonotelic is probably the most primitive form of excretion in aquatic animals. Among invertebrates various protozoa, coelenterates, polychaets, leeches, crustacea, echinoderms, cephalopods, pelyceps and some gastropods are essentially ammonotelic. The fresh water teleosts (carps and cat-fishes) and the amphibian tadpole larva are the only vertebrates exhibiting ammonotelic. However, a distinction may be made between **primary ammonotelic** and **secondary ammonotelic**. The excreting material is formed as ammonia and excreted as such in primary ammonotelic. In secondary ammonotelic the kidney or liver (as in *Helix*) contain a **urease** which breaks-down the first formed urea into ammonia, which is thus a secondary product.

Ureotelic animals are specially the vertebrates, although the earthworm *Lumbricus* has 89.4% urea in its ureine.

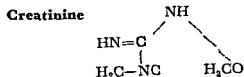
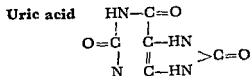
The highest percentage of urea in both blood and urine is

found in elasmobranch fishes (sharks, dog fishes and rays), in which the blood contains 2.5% of urea (which would kill any other vertebrate on account of **hyperuremia**). This is a special mechanism, explained later, for osmoregulation in sea water. Adult amphibians are all ureotelic, the synthesis of urea being done in the liver; whereas in elasmobranchs urea can be synthesized in any tissue of the body except the brain and the blood.

SOME NITROGEN EXCRETORY PRODUCTS



Guanine

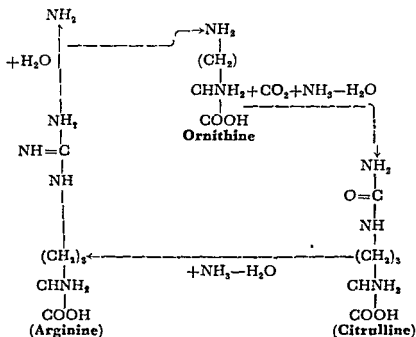


ORNITHINE CYCLE

Ureotelic animals, such as Lamellibranchiata, fishes, adult

amphibia, Dipnoi and mammals, convert ammonia into urea, eliminated in the urine, conversion is in the following steps called ornithine cycle :—

- (1) **Ornithine**: (amino-acid), reacts with ammonia and carbon dioxide to give **citrulline**.
- (2) This combines with one more NH_3 molecule to become **arginine**.
- (3) With the addition of one water molecule, arginine breaks into **Urea** and **Ornithine**, in presence of the enzyme **arginase**.



Some marine fishes, such as sculpin and the flounder, excrete almost 23% of total N_2 as creatinine. Trimethyl amine has been demonstrated in the urine of fishes (ophius, 19%, Carrasius, 16.8% and Sculpin 23%).

Characteristics of normal Human Urine

Volume....1,500 ml/24 hours
or 1 ml/per minute

total 60 gms/24 hours

solids

S. G.1,020

pH.6 (acid)

Composition

Urea.....30 gms

Uric acid.....0.7 gms

Ammonia.....0.7 gms

Creatinine.....1 gms

NaCl ... 15 gms

Phosphate (P_2O_5).....3 gms

Sulphate(SO_4).....2 gms

Nitrogen excretion has taken two evolutionary trends, both of which involve purine metabolism :—

- (1) the end products of protein and purine catabolism lead to the formation of ammonia, urea or uric acid ;
- (2) degradation of urea to ammonia, in presence of certain enzymes (urease, uricase *etc.*), the chain being broken at various points in both the vertebrates and invertebrates, *e. g.* as guanine, creatinine, allantoin and trimethyl amine.

OSMOREGULATION

There is no life without water. This is because water is the prime carrier of all the essential substances required for life function of the cell or the organism. **Osmoregulation** in animals is the control of osmotic pressure and water balance of the body. The fluids in cells of any animal as also the body fluids have a more or less constant **osmotic pressure** (O. P.), which has to be constantly and actively regulated (*e. g.* the O P of human blood is 6.7 atmospheres, which is equal to a pressure of a column of water 230 ft. in height). All living cells have a membrane covering, which is semipermeable (dialysing membrane) or has a differential permeability for water and solutes. Therefore the

O. P. inside body cells must be in equilibrium with the surrounding body fluids.

If we place red blood cells of man in a solution of about 160 milimolar NaCl, which is osmotically equivalent to plasma, then it retain its size and shape. This is because the cell is **isotonic** (same O. P.) with the salt solution. But if placed in a more dilute solution of NaCl, water enters the R. B. Cs and they swell. If immersed in pure water the cells swell and burst (haemolysis), being **hypertonic** (having higher O. P.) to the surrounding water. If the R. B. Cs. are placed in a higher concentration of NaCl than 16 milimolar, water leaves the cell and it shrinks (the cell being **hypotonic** (lower O. P.) to the surrounding salt solution.

This can be better understood in the simple experiment of placing sugar solution in an inverted thistle-funnel in water with a dialysing parchment membrane covering the funnel mouth (Fig. 65).

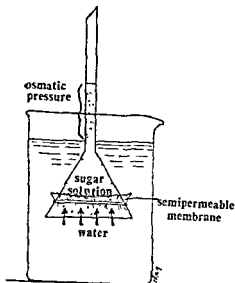


Fig. 65. Experimental demonstration of osmosis. (The height by which the solution rises equals the pressure by which the water enters the concentrated sugar solution.

The experiment shows the rising up of the sugar solution in the tube of the thistle-funnel, which goes on rising until the molar

concentrations of the two solutions have equal osmotic pressure. The pressure of the column indicates the O. P. of the solutes now in equilibrium.

We cannot, however, determine **Osmotic pressure** accurately by this method since there is no perfect dialysing membrane, known, which would allow only water to pass through into the thistle-funnel. Therefore the exact O. P. of a solution is determined by the depression of freezing point (Δ) caused by the solute. The depression of freezing point (Δ) of sea water is 2°C , i. e. -2°C when compared to the 0°C freezing point of fresh water. It is not surprising therefore that the blood and body fluids of most invertebrates which live in the sea have the same depression in freezing point (i. e. they are **iso-osmotic** with the surrounding sea water).

Shore and estuarine invertebrates have to withstand a varying osmotic pressure (within a short range) as the surrounding water changes its salinity. Such animals are called **stenohyaline** (steno=short, haline=salt). Such regulation of O. P. is done by secretion or absorption of salts through special organs (such as gills) since the body surface of an animal is not sufficiently permeable to salts. Difference in salt concentration can only be maintained by an active regulation, which is called **ionic regulation**.

In contrast such animals which have to face a large range of salinity are termed **Euryhaline**, e. g. the eel and the salmon. Animals which can regulate O. P. according to changing environment are called **poikilosmotic** animals e. g. marine eggs and protozoa, most molluscs, and all echinoderms. Other groups of animals, capable of maintaining a constant internal O. P. whatever the outside condition, are termed **homoiosmotic**, e. g., the fishes eel and salmon, (the eggs of which are however poikilosmotic—eel laying eggs in the sea and salmon in fresh water).

OSMOREGULATION FROM SEA TO FRESH WATER

Active osmoregulation can be seen in such poikilosmotic marine invertebrates (e. g. crustacea) which invade estuaries and

In the marine fishes, the hypertonic medium causes rapid loss of body water (exosmosis), to compensate for which the fish drinks more sea water. Both water and salts are absorbed by the intestine. The water thus absorbed makes up for the water loss. The salt cannot be excreted through the kidneys since urine of a higher concentration than sea water is not possible. Therefore, marine fishes excrete the excess salt absorbed, through special salt secreting cells evolved by the gills. This salt excretion is from a lower O. P. of the blood to a higher O. P. outside (hypertonic medium). It is therefore, an active transport requiring energy.

(It is unfortunate that man has no such special salt secreting organ and therefore drinking sea water may even be fatal for him, which has given the well known phrase for sailors "water water everywhere, not a drop to drink").

Osmoregulation in Fresh Water Fishes (Fig. 67).

In the fresh water fishes, water enters the body (endosmosis) due to the higher O. P. of blood than the surrounding fresh water.

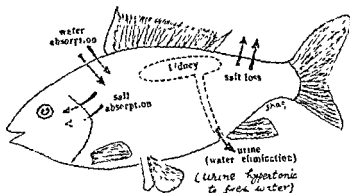


Fig 67. Osmoregulation in fresh water fish.

(It absorbs water, as its blood has higher salt concentration than the fresh water around it, excess water being removed as urine. Salt lack is made up by salt absorption through gills. (After Nielsen)

Therefore, fresh water fishes have to get rid of this continuously invading extra water by the kidneys; the kidneys of fresh water fishes having a far larger number of glomeruli than the kidneys of

blackish faeces, passed out of the cloaca (e.g. *Uromastix* and *Phrynosoma* in the deserts and poultry in the farm).

All mammals must drink sufficient water as they are homoiothermal, and evaporation is one of the main-stays of temperature control. Even the loss from the lungs is high, an average man losing 400 gms of H_2O daily in his expired air as water vapour. Similarly 15 gms/day are lost in sweat on a hot day; about 100 gms in faeces and 1500 gms/day in urine. (The volume of urine is however controlled by an anti-diuretic hormone ADH, released by the posterior pituitary in response to increased O. P. of the blood in dry atmosphere; no water is reabsorbed by the urinary bladder as otherwise commonly supposed. On the other hand when blood becomes diluted by more fluid intake, less ADH is released from the pituitary and urine volume is increased).

SOME PECULIAR OSMOREGULATORY ADAPTATIONS

The desert kangaroo rat (*Dipodomys*) is remarkable for not only living without drinking water for as long as six months, but for its capacity to produce a very small amount of extremely concentrated urine, which has two times the concentration of sea water. The kangaroo rat is therefore the only mammal which can drink sea water with impunity, which would poison other mammals. Possibly it is the only vertebrate which has such powerful kidneys to excrete high amounts of salts. However, the kangaroo rats body contains as much water as other mammals (average 66%). This body water is maintained by the water of oxidation produced even from the dry foods they eat. The kangaroo rat has no sweat glands, very little evaporation from the lungs, and a low water content in faeces and urine.

Another deserticolous mammal presenting a similar situation is the camel. The kangaroo rat comes out only in night and stays in under-ground burrows during the day; while the camel has to travel in the scorching heat of the desert day. The camel does not store any large amount of water in water cells (in the stomach) as commonly believed nor does it store water in the hump, which is pure fat. The so called water cells contain food fermenting fluid, which has the same O. P. as blood (not water). This fluid is absorbed in almost the same way as in our own stomachs as required. The other source of water in long journeys

is from fat metabolism of the hump—oxidation water. Thirdly, the evaporation of sweat, to control temperature, is reduced by allowing the body temperature to rise up to 41°C before sweating (early morning temperature of camel— 34°C , noon temperature— 41°C compared to 37°C of man, morning, noon and night). Finally, dehydration tolerance is 20% of body water in most mammals, but the camel can afford to loose over 40% body water, when other mammals would die. Thus after a long desert journey the camel may drink almost $1/3$ rd of its body weight of water in order to recoup the water loss.

The aquatic mammals and birds, such as seals, whales and penguins, do not drink sea water as commonly believed. They solve their water problem by eating large quantities of fish, which not only have a high water content, but an O. P. of about $1/3$ rd that of sea water. They have, however, specialized in producing rather concentrated urine, gaining more water from the fish, than loosing through urine, evaporation and respiration. The 80 feet long baleen whales feed on planktonic crustacea, which are almost 80% water; while the walrus eats clams and mussels containing still higher amount of water. However, since they cannot drink sea water, they have water conservation by producing concentrated urine, concentrated milk (having 40% fat content) and absence of perspiration.

Sea-birds (gulls, and penguins) have a special salt excreting gland in the head that excretes concentrated solution of NaCl. The salt excretion flows through the salt gland duct into the nasal cavity, and falls off through the beak. Marine alligators, crocodiles, turtles and tortoises, have also developed a salt gland close to the eye, its duct opening at the corner of the eye. (The 'crocodile tears' are therefore only a means for excess salt excretion). Tears are shed for osmoregulation and not emotion.

Thus in the case of these land vertebrates gone back to sea, the extra salt imbibed with the food is removed by various additional mechanisms, the inefficiency of the primary kidney mechanism in sea water reminding one of their land ancestry.

Chapter VII

INTEGRATION (NERVOUS SYSTEM)

Every animal is excitable or irritable, and perceives stimuli, translating them into nerve impulses which result in reactions. Even the simple *Amoeba* is excitable and irritable i. e. sensitive to stimuli both external (exteroceptive) and internal interoceptive). Here there is no nervous system at all, but the protoplasm exhibits irritability. In other protozoa such as ciliates (*Paramecium* *Stylonchia*) there is a specialised neuro-motor apparatus in the ectoplasm effecting perception of stimuli and co-ordination of impulses to cilia for synchronous and metachronous movements.

The simplest type of nervous system is found in the coelenterates, where there is a nerve-net connecting one cell with many others. This kind of nerve net is also found in localised parts of echinoderms, foot and labial palps of mollusca, enteropneusta, ascidians and also in the small intestine and blood vessels. The cells of the nerve-net are both receptors and effectors and no sensory or motor nerves are differentiated, nor is the central nervous system evolved yet.

In all these cases conduction is diffused, with complete absence of polarity; and a stimulus applied at one point reaches other points in the animal in all directions. The only polarity exhibited is in the sea-anemones, where a centripetal (from tentacles to mesentery) and a centrifugal (from mesentery to tentacles) polarity is obtained. One nerve cell, called a receptor, picks up a stimulus and transmits an impulse along a sensory or afferent fibre to a junction between the afferent and the effector cells. The passage of an impulse through a synapse is always unidirectional.

NERVE IMPULSES

A nerve can be stimulated by any changes in its environment, e. g., pressure, heating, chemicals *etc.* Such stimuli are converted into nerve impulses, which pass along the nerves independent of the type of stimulus.

A nerve impulse passes along a nerve fibre involving both chemical and electrical changes and requires the presence of oxygen. In the resting fibre the exterior of the semipermeable sheath has a positive charge with excess of Na^+ ions, while the interior has a negative charge with fewer K^+ ions. Hence the fibre is polarised. The impulse passes along the nerve fibre neutralising this electric charge. The role of the Na^+ and K^+ ions is to produce an action potential (current flow) sodium ions moving inwards and potassium ions outwards (Fig. 68). This creates a

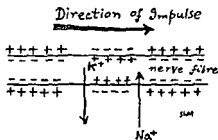


Fig 68 . Diagrammatic representation of the ionic transport in a nerve fibre during an impulse passage. (After Hodgkin)

positive charge in the interior and a negative charge in the exterior. After the passage of the impulse the fibre gets depolarised and cannot carry another impulse for some time, until the movement of K^+ and Na^+ ions re-establish polarisation.

Although the polarisation is due to shifts in permeability of Na^+ and K^+ ions the energy for entry of Na^+ and K^+ is due to the chemical action of splitting of thiamine and its recovery by glycolysis. An impulse travels at a uniform speed and with the same intensity throughout a fibre.

An impulse causes the finely branched ends of an axon (end branches) to produce a chemical **neuro-humor** **sympathin**, (a substance like adrenalin) which releases **acetylcholine** in the synapse. Presence of acetylcholine continues to stimulate the next nerve cell until an enzyme, choline esterase, inactivates it. Thus without acetylcholine the progress of the impulse would automatically stop. A drug **curare** if injected into a nerve fibre blocks the passage of nerve impulses by preventing the production of sympathin and acetylcholine.

VELOCITY OF CONDUCTION

The velocity of conduction varies in different neurons, being faster in myelinated fibres than in non-myelinated ones. In vertebrates the velocity is faster in thin fibres with thick sheaths (*e. g.* 4 μ fibre of cat nerve) whereas in invertebrates it is fastest in thick fibres with thin sheaths (*e. g.* 650 μ squid giant axon fibre). Both have the same impulse velocity of conduction at 25 m/sec.

The velocity of nerve impulses in some animals is: *Hydra* nerve-net, 0.1 to 0.2 m/sec; *Aurelia*, 0.5 m/sec; sea-anemone, 1m/sec; lobster, 6 to 12 m/sec in giant fibres; earthworm, 30 m/sec in giant fibres; frog, 20 to 30 m/sec; carp fish, 47 m/sec, Trout fish, 50 m/sec and most mammals 120 m/sec.

EVOLUTION OF NERVOUS SYSTEMS

The first differentiation into central and peripheral nervous systems occurs in flat-worms and annelids, the **central nervous system** comprising of one or more pairs of anterior ganglia or 'brain' and one or more ventral nerve cords extending posteriorly. The annelids, arthropods and molluscs have supra-oesophageal and suboesophageal ganglia connected and forming a 'nerve ring'. The **peripheral nervous system** consists of nerves arising from the brain and ventral nerve cord, and supplying the various organs of the body, the nerves usually arising from ventral ganglia.

Besides the bilaterally symmetrical nervous system of flat-worms, annelids, arthropods and molluscs except gastropoda

where torsion make it asymmetrical the echinoderms have a radially arranged nervous system conforming to their radial symmetry.

The highest evolved nervous system is present in the verte-

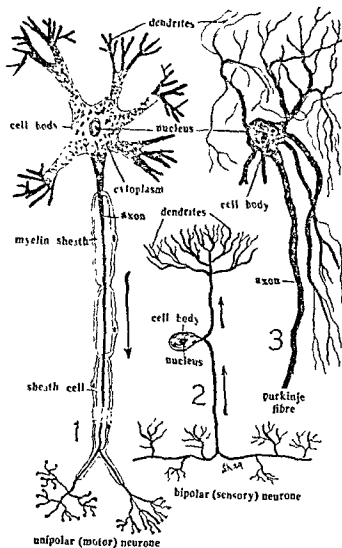


Fig. 69. Type of units, Neurones, the nervous system :

1. A unipolar neurone (impulse travel-
 ing through a neuron).
 2. A bipolar sensory neurone (impulse travel-
 ing through a neuron).
 3. A Purkinje fibre (impulse travel-
 ing through a neuron).

brates where it is divisible into five components: (i) the brain

(ii) the spinal cord (constituting the **central nervous system**); (iii) the cranial nerves, (iv) spinal nerves (constituting the **central peripheral nervous system**); and (v) the **autonomic nervous system** consisting of **sympathetic** and **parasympathetic** nerves.

Vertebrate neurones (Fig. 69).

The structural unit of the vertebrate nervous system is the **neurone**, which is the most specialised cell. Neurones have lost the ability to reproduce. The approximate number of neurones present in the nervous system of man is about one billion and about half of these are lodged in the cerebrum. This number remains constant from young to old age in all vertebrates. Since these cannot multiply or be replaced, nature maintains an enormous excess of neurones, only a fraction of the total number being utilized for the general activities of the animal at one time. A neurone possesses two special properties: (i) to react to stimuli; and (ii) ability to conduct an excitation or nerve impulse with high velocity. In the larger animals including man, a neurone process may be a metre in length, though less than a mm in width.

The neurone has a large **cell body** which is always located in the central nervous system or the peripheral ganglia. From the cell body arises a long main process the **axon** passing along nerves extending through the body of the animal. The other cell processes are shorter and much branched, called **dendrites**. Bundles of cell processes are associated as **white matter** in brain and spinal cord the whiteness being due to myelin. The neurone cell bodies, without myelin, are located in the **grey matter** only and are thus central in the spinal cord and peripheral in the brain. Neurones may be **unipolar** (motor with one axon, **bipolar** (sensory with two axons) or **multipolar** (with many axons *e. g.* Purkinje fibres of the cerebral cortex).

REFLEX ARC

Besides being the structural unit of the nervous system, a neurone is also a functional unit. It conducts the nerve impulse through a pathway, from receptor to effector, called a **reflex arc**.

(Fig. 70). Every receptor is supplied by a sensory (afferent)

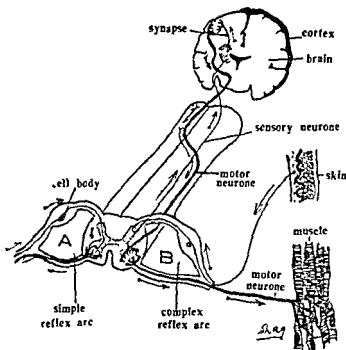


Fig. 70. Reflex arcs :
A—Simple reflex arc.
B—Complex reflex arc.

nerve; and stimulation of a receptor effects a nerve impulse which travels inward over the sensory dendrites into and out of the sensory neuron's cell body. The impulse then passes into the spinal cord or brain by way of the axon of the sensory neurone. In its path the impulse through a number of connecting multipolar neurones. Then the impulse is transmitted through a synapse into a motor (efferent) neurone, which in turn passes its axon into the effectors (muscles, glands *etc.*) for reaction. The simplest of reflex arcs is the common knee jerk in man. In this only one connecting neurone lies between the sensory neurone on one side and motor neurones on the other.

REFLEX ACTION

Each reflex action covers a reflex arc may be defined as an involuntary response of a muscle or gland to the stimulation of a

muscle or gland to the stimulation of a sense organ. A few examples of reflex action are: constriction of pupil in bright light (Fig. 71), blinking of eye at sudden, approach of an object; leap-

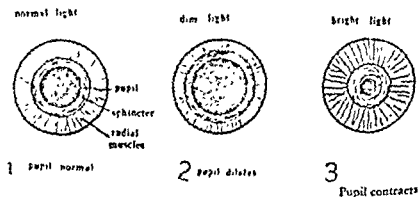


Fig. 71. Pupillary reflexes.

ing reflex in a decapitated frog (Fig. 72); flexion of limbs of a



Fig. 72. Leaping reflex in a decapitated frog.

spinal frog when stimulated by a prick (Fig. 73); salivation due to sight, smell or taste of food *etc.* (A running hen if decapitated, continues running for a considerable distance without a head—pinal reflex).

Receptor endings are of three types:—

- (1) **exteroceptive**, noting changes in the external environment;

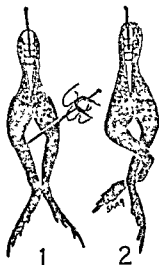


Fig. 73. Flexion of legs in a frog with only hind limbs and a portion of spinal cord intact.

- (2) **interoceptive**, sensitive to changes in the internal environment; and
- (3) **proprioceptive**, feeling, tension, pressure and orientation. Thus, broadly, three kinds of reflexes may be recognized; (i) **exteroceptive reflex**, primarily protective in character; (ii) **interoceptive reflexes**, playing an important role in the control of activities of internal organs; and (iii) **proprioceptive reflex**, largely concerned with maintenance of posture and equilibrium.

Types of reflex arcs according to their responses to stimuli):

Reflex arcs, are of six types:

- (1) **Simple reflex arc**: stimulus → receptor (sense organ)
→ sensation → afferent neurone → sensory impulse

body in dorsal root ganglion \rightarrow spinal cord \rightarrow synapse \rightarrow efferent neurone \rightarrow motor impulse \rightarrow effector (muscle or gland) \rightarrow reaction (*e. g.* knee jerk reflex in man, constriction of pupil in bright light).

- (2) **Compound reflex arc:** is one in which an impulse entering one sensory neurone influences several motor neurones through intermediate adjustor neurones (*e. g.* wringing the hands when the toe is hurt).
- (3) **Co-ordinated reflex arc:** is one in which a number of muscles respond in an orderly fashion to produce a useful reaction or movement. These are usually modified through association neurones extending to other parts of central nervous system (*e. g.* reflex avoiding a speeding car).
- (4) **Convulsive reflex arc:** is one where a number of muscles respond to an intense sensory stimulation in an unco-ordinated fashion. This produces a disorderly and useless movement, usually through spinal conducting tissue (*e. g.* produced by a third degree burn or electric shock, convulsive action in insanity).
- (5) **Chain reflex arc:** these are such that act in a sequence, the response of one becoming the stimulus for other (*e. g.* a kick on the leg results in a box on the ear of the kicker).
- (6) **Conditioned reflex arc:** produce complex actions, performed by reflex due to repeated performance of a chain act (*e. g.* cycling, typing, avoiding obstacles, hunger produced by ringing of dinner bell).

Reflex thus may be cerebral (Fig. 74), or spinal, unconditioned, superficial or deep, normal or abnormal, uncrossed or crossed (stimulation of one side of body causing reflex response on the opposite sides, *e. g.* siphons of *Herdmania*).

In invertebrates the reflex action involves only one or two neurones, but in all vertebrates at least three neurones are present, and at least one intermediate (connecting, associative, or adjutor)

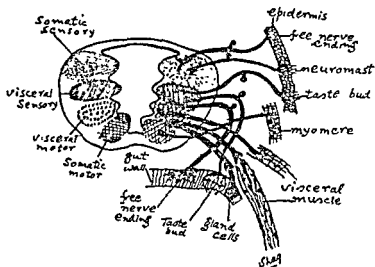


Fig. 74. The neural pathways in the cerebral reflex arc. (Cerebral Nerve Component).

(After Goodrich)

neurone is utilised. In mammals special **return impulses** from the cerebral cortex to the spinal cord are conveyed by special cortico-spinal tracks. Several pathways of conduction provide a mechanism for impulses to be conveyed from a lower level (spinal cord) to a higher level (brain) and *vice versa*. These mechanisms render possible the closest co-operation between parts of the central nervous system and the performance of extremely complex activities in man.

CEREBRAL INHIBITION

Reflexes are caused by excitation from a specific stimulus ; but a reflex action can be inhibited by nerve impulses coming from cerebral cortex, which is the highest centre in the brain. Thus a balance is maintained between excitation and inhibition, to keep the animal in a state of normal activity.

Functions of Brain and Spinal Cord

The main functions of the spinal cord are as follows :—

1. It serves as a centre for spinal reflexes ;

2. acts as a pathway for conduction of afferent impulses reaching various levels in the brain ;
3. serves for passage of efferent passages from different motor centres in the brain to the efferent neurone in the spinal cord ; and
4. the passage of efferent impulses into the effectors through the efferent neurones.

The functions of brain (with special reference to mammals) are as follows :—

The large **cerebral hemispheres** (cerebrum), the largest part of the brain in vertebrates, are concerned with the reception and correlation of afferent impulses, from the sense organs ; and the initiation of motor impulses to voluntary muscles, responsible for movements. The cerebral hemispheres also pass voluntary impulses into the spinal cord. Above all the cerebral cortex segregates the sensations arising from stimulation of different receptors of the body. It analyses, organises and integrates the impulses into various patterns of co-ordinated activity exhibited by the vertebrates in general and man in particular.

All sensations (except smell) are received by the thalamus from which ascending fibres pass to various regions of cerebral cortex. A narrow strip of cortex in the front part of parietal lobe is the seat for reception of cutaneous senses, such as touch, temperature or pressure (Fig. 75). Anterior to the **fissure of Rolando** in the frontal lobes, lie the three successive areas, **motor cortex**, **premotor cortex** and the **seats for eye movements** (responsible for control of body muscles). Just ventral to *Sylvian fissure* in the temporal lobe lies the seat of hearing or **acoustic centre** ; while ventero-lateral to the frontal lobe lies a small area of taste, smell and flavour (**gustatory**

centre). The centre for vision lies at the extreme hind end of the cerebrum in the occipital lobe. Therefore the arrangement is surprisingly upside

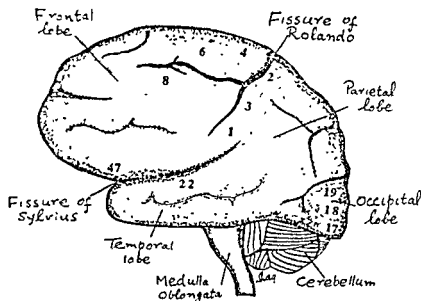


Fig. 75. Major cortical centres in man.
 1, 2, 3—Areas of cutaneous sense.
 4—Motor cortex.
 6—Premotor cortex.
 8—Eye movement centre.
 17-18—Visual centre.
 19—Eye movements.
 22—Acoustic centre.
 47—Gustatory centre.

down; *i. e.* sensation from the lower parts of the body is received at the upper end and the sensations from the head are received at the very bottom of the cerebrum. Further, all the fibres over which these sensations are transmitted are crossed over *i. e.* they are from the opposite side of the body. It is apparent, therefore that injury to the right side of the cerebrum causes paralysis or malfunction of the left side of the body.

The **olfactory lobes** are the primary seats of smell; they are extremely large in animals which are smell feeders *e. g.* sharks, mole, dogs *etc.*

Cerebellum is small in the lower mammals (*e. g.* squirrel) but becomes well developed in the higher ones, being most developed in man. It is connected to other parts of the nervous system by afferent as well as efferent pathways. Afferent neurones conduct impulses to the cerebrum or the spinal cord, while the efferent impulses are conducted away from the brain or through the spinal cord. Thus the cerebellum co-ordinates both sensory and motor functions, combining the various muscle contractions into organized body motions. An important function of the cerebellum is to control the tone of skeletal muscles and the maintenance of reflex equilibrium of the body.

The ventral connecting part between medulla oblongata and the lobes of brain already discussed, is the **diencephalon**, the **thalamus** of which serves to guide cerebellum in carrying out voluntary movements. It also serves for the recognition of certain large sensations, such as extremes of heat, cold, pain and wide amplitude body movements. In the main, it is an important relay station in the ascending pathways of impulses which terminate in the cerebral cortex.

The **hypothalamus** contains the **optic chiasma** in which partial decussation of optic nerve fibres from the retina occurs.

Physiologically the hypothalamus contains a constellation of nervous **nuclei** constituting the chief integrating centres of the autonomic nervous system. Connected with it is the hypophysis (pituitary which will be dealt with in a later Chapter) forming an important **neuro-endocrine** system, called the **hypothalamo-hypophyseal complex** (Fig. 76).

The **pineal gland** or **epithalamus** has a probable endocrine function, while the **metathalamus** serves as a relay station in the auditory pathway which extends from the acoustic labyrinth to cerebral cortex.

The **optic lobes** in lower vertebrates are only two, **corpora bigemina**, while in mammals there are four lobes, **corpora quadrigemina**. They are primarily concerned with sight and their

removal causes total blindness. It should be pointed out that removal of the thalamus and diencephalon (with optic chiasma) also causes total blindness. It is surprising that only the anterior

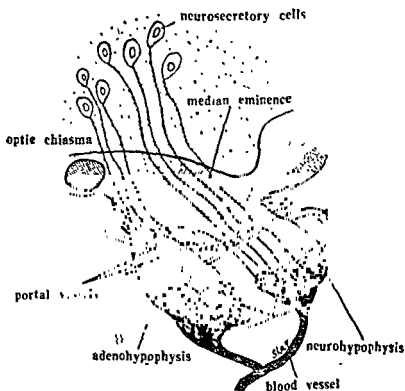


Fig. 76. Neurosecretory cells in Hypothalamo-hypophysial complex of mammal. (After Wessells)

part of corpora quadrigemina is concerned with sight; the posterior part has now been found concerned with hearing. (The mole has rudimentary anterior corpora and has poor sight, while the squirrel has large anterior corpora, since it is a sight feeder).

The ventral part of the midbrain contains nerve pathways by which impulses from cerebellum reach the voluntary musculature and effect the 'muscle sense'.

The medulla oblongata contains the so-called vital centres of the body which are of fundamental importance in maintaining

life. These are: (i) **respiratory centre**; (ii) the **heart beat centre**; (iii) **calibre controlling centre** of the blood vessels; (iv) the **centre of nerve tracts** connecting the spinal cord with the brain; (v) **deglutition centre**; and (vi) **cough and vomiting centre**. Destruction of these centre causes death.

For example when a man is hanged, he does not die of suffocation. What actually happens is that the odontoid process of the second vertebra (axis) smashes through the septum transversum of the first vertebra (atlas) and destroys one or more vital centres in the medulla oblongata, causing instant death.

PERIPHERAL NERVOUS SYSTEM

This system consists of nerves given off from the brain and spinal cord. Accordingly two types of nerves, the **cranial** (see Table) and the **spinal** are recognized. The cranial nerves, unlike the ten in lower vertebrates are twelve in mammals.

The cranial nerves differ from the spinal nerves in some important respects: (i) there is no spatial regularity (ii) they arise from a single root (either dorsal or ventral); (iii) the purely sensory nerves from sense organs bear no ganglia; (iv) embryologically they do not have a similar origin; (v) some are strictly motor, some strictly sensory, while others mixed; and (vi) only some of the cranial nerves connect with the sympathetic division of the autonomic system.

The spinal nerves are mixed nerves and are variable in the vertebrates, but in mammals there are 8 cervical, 13 thoracic, 6 lumbar, 3 sacral and a variable number of caudal nerves. Typically spinal nerves issue segmentally and separately almost equidistant from the spinal cord; but usually some nerves are grouped together in parts of the body to form a **plexus**. These are: (i) **cervical plexus** formed by the first 4 or 5 cervical nerves; (ii) **brachial plexus**, formed by the last three cervical nerves; (iii) **lumbar plexus**, formed by the last four lumbar nerves; and (v) **sacral plexus**, formed by the last three sacral nerves.

TABLE OF CRANIAL NERVES

No.	Nerve	Origin	Distribution	Function
I.	Olfactory.....	Olfactory bulb	Schneiderian membrane of nose.....	Special sensory
II.	Optic.....	Optic chiasma	Retina of eye.....	—do—
III.	Oculomotor.....	Crura cerebri just anterior to pons	Inferior oblique, medial, superior and inferior rectus muscles.....	Motor
IV.	Trochlear.....	Posterodorsal margin of mesencephalon	Superior oblique muscle....	—do—
V.	Trigeminal			
(a)	Ophthalmic	Medulla, at posterior margin of pons	Nose, upper eyelid, skin of cranium lacrymal glands....	Mixed sensory
(b)	Maxillary	—do—	Upper teeth, lips and cheek.....	Sensory, motor, and special sense
(c)	Mandibular	—do—	Motor fibres to muscles of mastication; certain skin muscles; sensory fibres from papillae of tongue; sensory fibres from mandibular teeth	—do—

No.	Nerve	Origin	Distribution	Function
VI.	Abducens	Medulla, posterior to Trigeminal	Lateral rectus and adjacent parts	Motor
VII.	Facial	Posterior margin to pons	Skin muscles of face; diaphragmatic, parotid and submaxillary glands	Motor
VIII.	Auditory	Medulla, posterior to Facial	Labyrinth of internal ear....	Special sensory
IX.	Glossopharyngeal	Medulla, with Vagus	Base of tongue, pharynx and soft palate	Sensory, motor and special sense
X.	Vagus	Lateral part of medulla	Pharynx, trachea, larynx, oesophagus, heart, lungs, and stomach.....	Motor and sensory
XI.	Spinal accessory (in mammals)	Six or seven cervical roots connected to medulla	Sternomastoideus and trapezius muscles.....	Chiefly motor
XII.	Hypoglossal (in mammals)	Posterior to spinal accessory	Muscles of larynx, hyoid and tongue.....	—do—

AUTONOMIC NERVOUS SYSTEM

This system controls the functioning of the heart, blood vessels, alimentary canal, uterus, urinary bladder, lungs, liver, pancreas and various glands, in vertebrates. The entire system consists of a system of nuclei and fibre tracts in the brain and spinal cord, composed of afferent and efferent visceral, preganglionic and post-ganglionic neurones, as also autonomic ganglia and plexuses. The chief functions of the autonomic nervous system is to maintain a constant internal environment (**homeostasis**) with regard to concentration of salts, foods and waste products; osmotic pressure, gas tension, temperature *etc.* It has a close functional co-ordination with endocrine glands and thus it operates in emergencies producing responses favourable to the survival chances of the animal.

The autonomic nervous system consists of two parts:— (1) **Sympathetic (thoraco-lumbar)**; and (2) **Parasympathetic (cranio-sacral)**. The two parts have usually an antagonistic action. For both systems the chief controlling centre lies in: (i) spinal cord; (ii) brain stem; and (iii) cerebral cortex (**Fig. 77**).

Sympathetic System: The sympathetic part consists of ganglia and nerve fibres, passing out of the spinal cord along with various spinal nerves. A chain of ganglia (20-24 pairs in mammals) is present along both sides of the vertebral column. **Preganglionic** fibres arise from the grey matter of the spinal cord; each synapses with a cell in a **sympathetic ganglion** and emerges as a **postganglionic fibre** before innervating a body part. Usually a preganglionic fibre is shorter than a postganglionic one.

The sympathetic ganglia may be arranged as **cervical, thoracic, lumbar, sacral** and **caudal**.

The first or **superior cervical ganglia** send fibres into the vagus and sympathetic components, and also supply the pupil of the eyes, salivary glands and arterioles of nose and throat. Thus, they effect a controlling action on the heart, lungs; the di-

of the pupil, and dilation of arterioles of nose and throat. The middle cervical ganglia send fibres into the vagus and also the

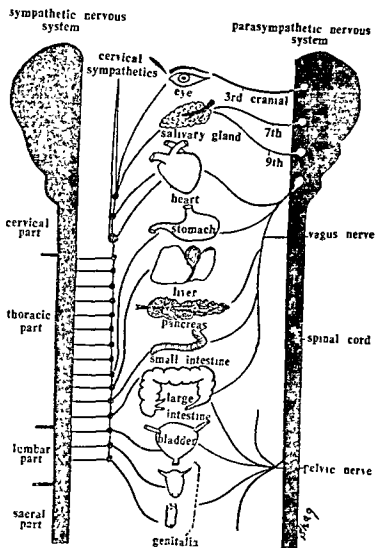


Fig. 77. The distribution of sympathetic and parasympathetic nervous (diagrammatic).

sympathetic chain. The inferior cervical ganglia lead into the

main sympathetic chain, running adjacent to the heart and descending aorta, which they innervate.

The **thoracic sympathetic trunk** is important since it give off a pair of splanchnic nerves near the diaphragm (in mammals), which penetrating it join a semilunar ganglion consisting of about 20 fused ganglia. Collectively they form the **solar plexus**, in conjunction with numerous nerve fibres that innervate the viscera, and control peristaltic contraction and secretions. (This is the spot which boxers often uses foully to paralyse the opponent—*hitting the belly below the belt*).

The **abdominal sympathetic trunk** passes posteriorly beneath the kidneys and ends in as many ganglia as there are the lumbar and sacral spinal nerves, sending fibres into a large **inferior mesenteric ganglion**, controlling the pelvic viscera.

Parasympathetic System: These fibres leave the central nervous system through IIIrd, VIIth, IXth and Xth cranial nerves and by way of IIInd, IIIrd and IVth sacral spinal nerves. Accordingly the parasympathetic system can be divided into a **cranial parasympathetic** and a **sacral parasympathetic** part.

Though the autonomic fibres are motor in nature, they have a definite reflex activity. There are, in fact, **spinal reflexes** for the autonomic system, such as *blinking*, *salivary juice secretion* etc.

As stated above the **sympathetic and parasympathetic parts** have usually an **antagonistic action** for *example*.

The importance of the autonomic system can be realised by the following everyday illustrations. For example, as soon as a fearful state ensues the following involuntary symptoms—

1. *drying of mouth;*
2. *palpitation & beating of heart;*
3. *increased blood pressure;*
4. *etc. etc.*

Organ/system/ function	Effect of sympathetic stimulation	Effect of para- sympathetic stimulation
---------------------------	--------------------------------------	---

Pupil of the eye Dilation

Constriction

Salivary glands Inhibition, resulting in less and thick secretion.

Stimulation resulting in much thick secretion.

Heart beat Increase in heart beat rate.

Decrease in heart beat rate.

Blood Pressure Increased by reducing the calibre of arterioles.

Decreased by dilation of arterioles.

Branchioles Dilation

Constriction

Gastric and pancreatic juice secretion None

Stimulation

Adrenalin secretion Increases

None

Bladder Storage reflex by relaxation of bladder wall and constriction of sphincter.

Voiding reflex by constriction of bladder wall and relaxation of sphincter.

Penis Ejaculation

Erection

Ilio-colon Contraction causing pain

Relaxation

Hair muscles Stimulated to erect hair on end.

None

B.M.R. Increased

None

The common stage fright is a similar phenomenon, by overstimulation of sympathetics, when the person may be literally struck dumb. The phenomenon of the drying of mouth in fear, was used hundreds of years back to spot a thief. The lined up suspects were threatened with dire consequences, if the thief does not confess ; a small pebble was put in the mouth of each suspect and taken after a very short time. The real culprits sonte come out dry whereas all others were wet with saliva. Here is an instance of sympathetic inhibition practically stopping the parasympathetic salivary secretion. Similarly sudden appearance of a fearful authority or phenomenon results in urination, specially in children. Stimulation of the parasympathetic fibres of vagus can reduce the heart beat in most mammals and completely stop in the turtle.

Chapter VIII

INTEGRATION (ENDOCRINE SYSTEM)

Functional integration of the animal body is brought about by two means: (1) nervous (already discussed, Chapter Seven); and (2) chemical and hormonal. In the first category fall such functions as: (a) quick adjustment; (b) muscular activities and correlation; and (c) responses to outward environment. In the second category are comparatively gradual functions such as: (a) growth; (b) metabolism; (c) adjustment of tissues and organs to one another; and (d) functional balance of all enzymes and even hormones themselves; all these are largely controlled by the **endocrine system**, secreting different hormones.

INVERTEBRATE HORMONES

It was only after 1928 that the existence of hormones in invertebrates was discovered. This was the finding of a substance formed in the eye stalks of the shrimp, which causes contraction of the chromatophores and is now found to be true of all crustacea which can change colour. This is comparable with the first discovery of hormone **secretin** in the vertebrates, essential for secretion of gastric juice. In the invertebrates the endocrine organs are small and different in form and location in the different groups. The groups in which endocrines have been clearly demonstrated are annelida, arthropoda and mollusca. There is enormous scope for future work in this field.

In general there are two points worth noting in invertebrate endocrinology: (1) there is a close connection between nervous system and endocrine system in invertebrates than in the vertebrates; (2) invertebrate hormones are different in chemical compo-

sition and function from vertebrate hormones. The identifiable vertebrate hormones in vertebrates are hardly three or four, *e. g.* adrenalin, noradrenalin, serotonin and acetylcholine, if it can be called a hormone. The injection of vertebrate hormones in invertebrates hardly affect their function.

In the **annelida** the only hormones known (without any nomenclature) are: (1) an **Inhibitory Hormone**, preventing sexual development of immature worm, produced by neurosecretory cells in the brain; (2) a **Regenerating Hormone**, influencing posterior regeneration in oligochaetes and polychaetes. Asexual reproduction and stolon formation in polychaetes is controlled by another hormone secreted by the proventriculus and not the brain.

In the **crustacea** the best known endocrine organs are in the eyestalks, the post oesophageal commissure, the pericardial wall and the sinus gland (enclosing eyestalk ganglia) which are the most potent sources of hormones. The chromatophores as also movements of the pigments of retina are controlled by the **sinus gland hormones**. Some have demonstrated a dibetogenic principle keeping the blood sugar above a minimum, in the sinus gland hormones. It has also three **Molting Hormones**. The **Pericardial Hormones** accelerate the heart beat.

The best known invertebrate hormones are those which control growth and molting in insects.

The main endocrine glands in **insects** are corpus allatum, pars intercerebralis, prothoracic glands and corpora cardiaca. The **corpus allatum** secretes an **Inhibitory Hormone** which prevents metamorphosis. (Giant silkworm larvae 6 inches in length, can be produced by transplanting corpus allatum of young larvae into the older larvae). The **pars intercerebralis** has a neurosecretion inducing molting and differentiation, and is thus antagonistic in action to corpus allatum hormone. The **prothoracic glands** secrete a **Growth differentiation Hormone (GDH)**, which is triggered off by another neurosecretory hormone

produced in the *pars intercerebralis* of the brain. In early larval life the *corpora allata* secretes an inhibitory hormone called **Juvenile Hormone** or **Status Quo Hormone (SQH)**, and thus removal of *corpora allata* is followed by premature pupation, metamorphosis and emergence of minute adults.

The queen bee produces a **Queen Substance** (hormone) which licked from her body by young workers inhibits the development of their ovaries. The arrest of growth in some insects called **diapause** seems to occur by a hormone from the suboesophageal ganglia. The **Corpora cardiaca Hormone** effects the chromatophore contraction.

In **molluscs**, specially in cephalopods and gastropods, hormones have been demonstrated which control the chromatophores and the development of gonads.

VERTEBRATE HORMONES

The main endocrine organs in vertebrates arranged antero-posteriorly in the body are: (I) **pituitary** (hypophysis), (II) **thyroid**, (III) **parathyroid**, (IV) **thymus**, (V) **pancreas islets**, (VI) **gastre-intestinal mucosa**, (VII) **adrenals**, (VIII) **gonadian tissues**, and (IX) an anterior accessory organ, **pineal body** (Fig. 78).

(I) PITUITARY HORMONES

Pituitary has long been called the master gland of the vertebrate body (Fig. 79). Usually this gland is divisible into three lobes, from fish upto man. In mammals the lobes are termed: (1) anterior lobe, which is glandular; (2) posterior lobe, which is smaller and nervous; and (3) the intermediate lobe, consisting of a small glandular mass lying between anterior and posterior lobes.

1. Anterior Pituitary (Pars Distalis) Hormones

These are three in the man viz. **Growth Hormones**, **Gonadotropic Hormones** and **Metabolic Hormones**. GH

(Growth Hormones) or STH (Somatotropic Hormones):

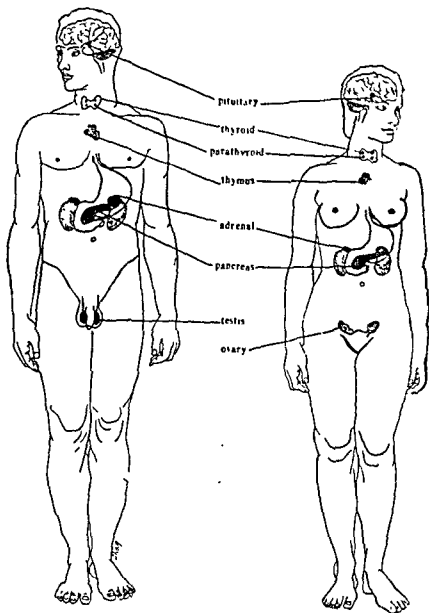


Fig. 78. Endocrine, hormone secreting, ductless glands of male and female humans.

(After Zuckerman)

These act as a direct stimulus to general growth. Overstimu-

lation (hypersecretion) of anterior pituitary causes gigantism,

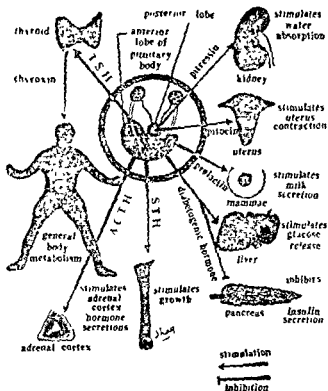


Fig. 79. Action of the pituitary hormones in triggering secretions actions of other organs.

while hyposecretion leads to stunted growth or dwarfism. Injection of GH stimulates growth in all classes of vertebrates.

Gonadotropic Hormones: Four main categories of these hormones have been identified: (a) the F.S.H. or Follicle Stimulating Hormone; (b) L.H. or Luteinising Hormone; (c) I.C.S.H. or Interstitial Cell Stimulating Hormone; (d) P.L. or Prolactin or Lactogenic Hormone.

F.S.H. causes ovum. L.H. cause is responsible for

formation. P.L. or Lactogenic Hormone is responsible for maintenance of corpus luteum and secretion of progesterone which activates milk secretion.

Metabolic Hormones: They have an indirect action: (a) **Thyrotropic Hormone** stimulates development and controls secretion of the thyroid gland; (b) **A.C.T.H. (Adrenocorticotrophic Hormone)** stimulates the production of steroids by the adrenal cortex which activates metabolism of carbohydrates; (c) **N.P.N. (Non-Protein Nitrogen Affecting Factor)** causes a striking drop in the N.P.N. of the blood, which is a diagnostic test made by injection of anterior pituitary extract. Thus it accelerates protein synthesis in the body; and (d) **Diabetogenic Factor** inhibits pancreatic islands from producing insulin.

2. Posterior Pituitary (Pars Nervosa) Hormones

Posterior pituitary secretes the complex hormone called **Pituitarin**. It contains two definite hormones: (a) **Pitocin (Oxytocin)**; and (b) **Pitressin (Vasopressin)**:

(a) **Pitocin** (has an oxytocic effect on smooth muscles of stomach, intestine and urinary bladder; but is most marked in the case of uterine muscles which signifies postnatal contractions of the uterus. It has also been held that the uterine contraction during copulation for internal transport of sperms may be due to pitocin.

✓ Vasopressin

(b) **Pitressin** causes constriction of nearly all blood vessels and its effects are: (i) action on the cardiovascular system, causing a rise in blood pressure; (ii) in mammals however, there is an **Anti-diuretic Factor Hormone (ADH)** present which acts on the kidneys by inhibiting water loss in the renal tubules i. e. stimulates water reabsorption in the renal tubules.

Extirpation or damage of posterior pituitary causes uncontrolled excretion of large quantities of dilute urine, a condition known as diabetes insipidus in man. It has been observed that the anti-diuretic effect is controlled by the neurosecretory cells in the hypothalamus, which respond to the concentration of chlorides or other solutes. Obesity can be reduced by injections of posterior lobe extract; and therefore obesity in man may be due to deficiency of posterior pituitary hormone.

According to one view the pars nervosa may not be an endocrine gland at all, but only a storage organ for hormones (neurosecretions) produced in the supra optic and para ventricular nuclei, from which nerve tracts supply the posterior pituitary. Therefore, instead of only hypophysis, the hypothalamus has an essential role in the secretion of pituitary hormones hypothalamo-hypophysial complex.

3. Intermediate Lobe (Pars Intermedia) Hormone

Intermediate lobe which is comparable to the pro-adenohypophysis of fishes is active and important in only poikilotherms. Its hormone Intermedin (MSH—Melanocyte Stimulating Hormone) causes extension of pigment granules of the chromatophores of the skin, producing changes in the skin colour. Its exact function in birds and mammals is not known. However recent evidence suggests that it effects melanin synthesis in mammals.

The pars tuberalis present at base of pituitary in fishes and amphibia has been shown to produce the 'W' substance that concentrates the pigment of the melanophore; and is thus antagonistic to the action of intermedin.

II. Thyroid Hormones

The secretion of thyroid has been called thyroxin, but it actually contains three hormones, for: (a) development; (b) growth; and (c) metabolism. Thyroxin is unique among hormones in that it is not easily digested and can thus be successfully administered orally.

(a) Developmental Factor: The developmental factor is dramatically demonstrated in thyroidectomised tad-

poles which prevents them from metamorphosing into frogs, and large nine inch long tadpoles can be obtained by feeding them on non-thyroid food upto ten weeks. On the other hand tiny tadpoles (with thyroid) fed on thyroid tissue are transformed into frogs, as small as flies in ten days. In mammals this factor effects normal postnatal development; and lack of thyroid hormones retards sexual and mental development.

(b) **Growth Factor:** Thyroid insufficiency in children results in cretinism, a condition of retarded physical, sexual and mental development; cretins having a low B.M.R., low heart beat rate, delayed eruption of teeth and often deaf-mutism.

(c) **Metabolic Factor:** This accelerates the B.M.R. and thus all bodily activities are heightened.

All these three factors isolated from thyroxin contain iodine (*viz.* iodothyroglobulin, di-iodotyrosine and thyroxin respectively). Thyroid takes up iodine or iodide from the food; oxidises it and incorporates it into a protein, thyroglobulin, which is stored in the gland and then split by a proteolytic enzyme to form thyroxin.

I.

the thyroid called exophthalmic goitre. This can be easily treated by continued administration of dilute potassium iodide solution. Hypersecretion causes hypermetabolism (by 100% up—Graves disease), the symptoms being increased heart beat, tremors, emaciation and protrusion of the eye balls. Hypo-secretion causes cretinism in children and myxedema. in which the of Ambystoma more can be Thyroxin in

III. PARATHYROID HORMONES

Parathyroids have been found to take over the function of thyroid in an emergency or an removal of thyroids. The parathyroid hormone called **Parathormone** is easily destroyed by proteolytic enzymes, when given orally. The hormone has the following six functions:—

1. Regulates calcium level of blood;
2. regulates inorganic phosphate in blood;
3. regulates urinary excretion of calcium and phosphate;
4. increases urinary output of water;
5. preserves normal excitability of neuro-muscular apparatus, as removal or damage of parathyroids causes irritability, muscular twitching, spasms and finally parathyroid tetany and death; and
6. deposition of bony tissues is regulated since an over secretion of parathormone leads to have softening, skeletal decalcification and may lead to a multiple fractures by minor injuries.

Parathormone and vitamin D : Maintenance of proper concentration of calcium and phosphate in the internal environment of the body. Adequate amounts of vitamin D must be available for the hormone to exert its characteristic effects.

IV. THYMUS

Thymus was thought to be a lymphoid organ for a long time, but its endocrine nature has been demonstrated recently. Experimental data show that feeding of tadpoles by thymus tissue retards metamorphosis but accelerates growth. It is largest in young animals (maximum size in man at two years age), while in adults it becomes smaller. Extract of thymus injected into rats has been shown to greatly accelerate development and sexual maturity.

V. PANCREATIC HORMONES

The islets of Langerhans (Fig. 80); secrete the hormone

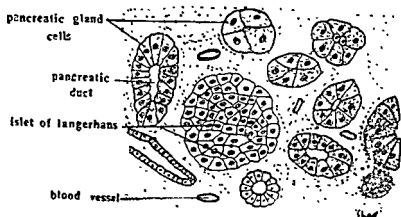


Fig. 80. Section of pancreas to show enzyme secretion lobules and insulin secreting islets of Langerhans.

Insulin, which is a vital hormone; extirpation or damage of pancreas causes death in all vertebrates. The essential functions of insulin are:

- (1) Prevents overproduction of sugar from protein and fat;
- (2) promotes storage and peripheral utilization of sugar by enhancing phosphorylation of glucose, which is a prerequisite to oxidation;
- (3) blood sugar level is lowered;
- (4) storage of glycogen in liver and muscle is promoted;
- (5) glycosuria (high sugar in urine) is prevented;
- (6) the rate of ketone body formation is reduced; and
- (7) elimination of nitrogen by kidneys is reduced.

Injectins of insulin have been found to increase the weight of animal, specially if it is diabetic.

The chief controlling factors for secretion of insulin are:
(a) stimulation of Xth nerve; and (b) concentration of glucose in

blood flowing through the pancreas. In short, there is more secretion of insulin, if there is hyperglycemia (above normal blood sugar) and less secretion if there is hypoglycemia (less than normal blood sugar)

Insulin is produced by the beta cells of the pancreas, while another factor Glucagon (some time referred to as a separate hormone) is produced by the alpha cells. The action of glucagon is to increase the blood metabolism of sugar by accelerating phosphorylation and break down of liver and muscle glycogen to yield glucose-1-phosphate. Diabetes mellitus caused by lack of insulin can be treated by the administration of insulin, which must be carefully regulated in amounts to prevent too much glucose being removed. This disappearance of glucose from the blood is by conversion into lactate, fatty acids, oxidation to CO_2 and synthesis to glycogen (called four line conversion of glucose).

VI. GASTRO-INTESTINAL MUCOSA HORMONES (Fig. 81).

The mucous membrane of the stomach and small intestine (not large intestine) play an important role in the regulation of gastro-intestinal enzyme secretion, as also the peristaltic movements of the gut. The gastro-intestinal hormones are: **Gastrin**, **Secretin** **Cholecystokinin**, **Enterogastrone**, **Villikinin**, **Duocrinin** and **Pancreozymin**.

(a) **Gastrin**: It is secreted by the pyloric mucosa of the stomach, and is liberated by the action of chemical substances (peptones, weak acids *etc.*) in the food. Gastrin is absorbed into blood and carried to gastric glands, where it causes copious secretion of gastric juice.

(b) **Secretin**: It was discovered by Bayliss and Starling in 1902, being the first hormone to be discovered. Secretin is secreted by the duodenal mucosa on stimulation by acid (HCl) chyme. It is conveyed to the pancreas and liver through blood causing copious secretion of pancreatic juice and bile into the duodenum. It also augments gastric secretion.

(c) **Cholecystokinin:** This hormone is secreted by the mucosa of the duodenum, liberated by fats and fatty acids. It stimulates contraction of gall bladder pouring bile into the duodenum. Gall bladder being

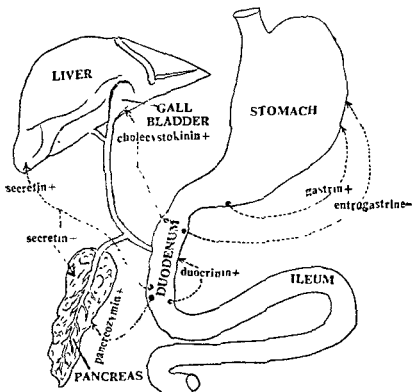


Fig. 81. Gastrointestinal hormones which regulate the secretion of digestive glands. (A plus sign indicates stimulatory action and a minus sign inhibitory action (Goroman and Bern).

absent in elephant, antiodactyla, rat and mouse cholecystokinin stimulates relaxation of the bile duct in these animals.

(d) **Enterogastrone:** It is secreted by the duodenal mucosa, and is liberated by the presence of fats and carbohydrates in duodenum; the hormone is conveyed to the stomach, where it inhibits gastric secretion and gastric peristalsis. Thus its action is antagonistic to that of gastrin. Similarly urogastrone which

is an excretory product of enterogastrone, inhibits secretion of pancreatic juice and is thus antagonistic to secretin.

(e) **Villikin**: This hormone is secreted by the mucosa of the small intestine. It promotes intestinal absorption by stimulating the activity of intestinal villi.

(f) **Duocrin**: It is produced by the duodenal mucosa and stimulates the production of **succus entericus** (intestinal juice) by the intestinal glands.

(g) **Pancreozym**: This hormone is secreted by the mucosa of the small intestine. It acts on the zymogen granules of the pancreas and increases the rate of enzyme output by the pancreas.

VI. ADRENAL CORTEX AND MEDULLARY HORMONES

The adrenal glands, like the other vital endocrine glands, such as pituitary, thyroid, pancreas *etc.* on extirpation or damage result in death. Each adrenal consists of two parts, the **adrenal medulla** and the **adrenal cortex**. The important hormones secreted by these glands are: **Adrenalin**, **Noradrenalin** and **Cortin** or **Interrenalin**.

(a) **Adrenalin**: Adrenalin secreted by the adrenal medulla is released intermittently under direct nervous control. Adrenalin is known as the **Emergency Hormone**, since it is secreted in large amount only during physiological stress, such as fear, pain, shock, extreme cold and asphyxia. Its action is immediate and potent (Fig. 82); but more temporary than that of other hormones. A dilution of one part in 400 million suffices for immediate physiological effects. Its primary mechanism of action is to reinforce and prolong the action of the sympathetic nervous system, working in conjunction with it. The functions of adrenalin are many:

- (1) Increase the strength and rate of heart beat;
- (2) constriction of peripheral arterioles causing a general rise in blood pressure;

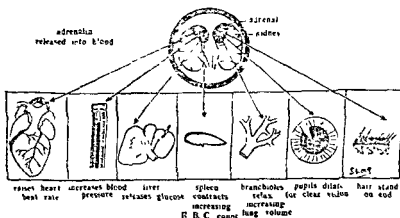


Fig. 82. Action of the hormone **Adrenalin** when released in blood.

- (3) dilatation of blood vessels of skeletal and cardiac muscles;
- (4) contraction of the spleen releasing more erythrocytes in circulation to carry more oxygen;
- (5) more rapid coagulation of the blood;
- (6) relaxation of bronchioles to allow increased oxygen supply;
- (7) increase in oxygen consumption and consequent heat production;
- (8) glycogenolysis (glycogen break down to lactic acid) in the liver and muscles;
- (9) relaxation of hepatic sphincter;
- (10) elevation of blood sugar level and thus postponement of fatigue;
- (11) decrease the activity of digestive peristalsis and contraction of the digestive sphincters;

- (12) relaxation of the bladder and contraction of its sphincter ;
- (13) contraction of erector pili muscles and elevation of hair ;
- (14) dilatation of the pupil , and
- (15) increase in secretion of saliva.

(b) **Noradrenalin (Arterenol)** · This is a second hormone secreted by adrenal medulla. Its functions are similar to that of **Sympathin** (substance produced at symphthetic nerve endings) and its action has similar, although weaker effects as adrenalin.

(3) **Cortin or Interrenalin** : It is a vitally important hormone essential for life, secreted by the adrenal cortex. Extirpation or failure of adrenal cortex causes upset in osmoregulation and to blood volume in the body. In man this causes **Addison's disease**, which is fatal unless cortin is injected. Its main functions are :

- (1) water and electrolyte balance in body fluids through its action on kidney tubules ;
- (2) control of blood volume ;
- (3) control of carbohydrate metabolism ,
- (4) exerts a control over lymphoid tissue (immunity bodies are released into the blood) ;
- (5) influences the development of sex organs and appearance of secondary sex characters ; and
- (6) speeds up developmental stages of the animal (hypersecretion of adrenal cortex causes such a precocious development in a child that he may look like an old person).

Adrenal function is almost entirely controlled by ACTH of the anterior pituitary. The adrenocortical hormones are all steroids, such as desoxycorticosterone, corticosterone and cortisone. Of late cortisone is being used for treatment of rheumatoid arthritis in man.

VIII. GONADIAN HORMONES

Gonadian hormones are essential for the production of germ cells in both male and female animals; besides which they regulate the proper development of the reproductive organs, and the development of the secondary sex characters (in conjunction with cortin).

1. Male Gonadian Hormones.—The male hormones generally called **Androgens** are elaborated and secreted in the blood stream by the **interstitial cells of Leydig** of the testes. Extirpation of the testes in young animals or in childhood (castration) prevents the appearance of secondary sex characters, the individual becoming a eunuch in man. The main male hormones are: (a) Testosterone; (b) Androsterone; (c) Isoandrosterone; and (d) Dehydroisoandrosterone.

(a) **Testosterone:** has the following functions:

- (1) stimulating the development of male accessory sex organs;
- (2) stimulating the activity and maintenance in functional state of testes and erection of penis.
- (3) development of normal male body form;
- (4) aggressiveness, voice and hairiness of the male; and
- (5) catabolism of fat in the body (specially subcutaneous fat).

(b) **Androsterone:** has similar functions as testosterone but is less potent.

(c) **Isoandrosterone:** is formed during metabolism and action of testosterone.

(d) **Dehydroisoandrosterone:** is also an effective male hormone, which has been isolated from the urine of male mammals and man.

2. Female Gonadian Hormones.—The female gonadian hormones are elaborated by the interstitial cells of the ovaries (like the testes), but other female hormones are secreted by the Graafian follicles in all vertebrates, and the corpus luteum and placenta during pregnancy in mammals. The main female hormones are: (a) **Oestrogen** or **Oestradiol**; (b) **Progestin** or **Luteal hormone**; (c) **Relaxin**; and (d) **Chorionic Gonadotropin**.

(a) **Oestrogen**: is the hormone which produces heat (oestrus) in female mammals and is secreted by the Graafian follicles also by the placenta. It has three important functions:

- (1) development of accessory sex organs in the female;
- (2) maintenance in functional state of the accessory sex organs; and
- (3) appearance of female secondary sex characters.

(b) **Progestin**: is produced by the corpus luteum in mammals and comes into play only after implantation. Its main functions are:

- (1) preparation of the uterine mucosa for implantation;
- (2) influencing development of mammary glands (which is later taken over by prolactin of the pituitary);
- (3) inhibition of ovulation and menstruation during pregnancy; and
- (4) maintenance of normal pregnancy. Progestin is also produced by the placenta).

(c) **Relaxin**: the third ovarian hormone is also produced by the interstitial cells of the ovary, which increases in late pregnancy. Its main functions are:

- (1) to relax the ligaments of the pelvic girdle, (and

therefore now used in creams for relaxing sprained ligaments);

- (2) to soften the vagina or vestibule to facilitate birth. (Relaxin is produced by the ovary alone).

(2) **Chorionic Gonadotropin:** is secreted by placenta alone. Its main functions are:

- (1) to supplement the action of hypophyseal gonadotropins (FSH, LHH and Prolactin) and is often called APL (Anterior Pituitary Like Hormone);
- (2) causes corpus luteum to persist; and
- (3) safeguards the status quo of placenta.

The sex of an animal is normally genetically determined, i. e. whether it is going to be a male or female. On the other hand gonadian hormones have been shown to affect the sex in amphibia, birds, and mammals. Abnormal secondary sex characters, such as development of breasts, reduction in size of testes and penis, loss of hairiness in the male, have been recorded several times in man by the introduction of female gonadian hormones. Only a few years back in a factory manufacturing female hormone pills a large number of workers started developing breasts, with accompanied pain in the pelvic region, and loss of manliness. This effect of oestrogens was by mere inhalation and contact with the fine hormone powder. The workers resumed normality only after months of androgen treatment. Castrated deer do not grow antlers, and no fructose normally secreted with the semen of bulls and bucks, is formed after castration. Characteristically both antlers and fructose are restored by testosterone. Similarly oestrogens injected into castrated young kangaroos causes the scrotum in front of the penis to be converted into typical female marsupium or pouch.

Androgens and oestrogens also play an important part in the general psychic and emotional life of both birds and mammals. Thus the maladjustments between husband and wife may be partly due to imbalance in gonadian hormones.

A hen may crow, a cock may lay eggs; boys may be changed into girls and *vice versa* by operation; and fierce bulls turned into

2. **The Pituitary Releasing Factor System**, located in the hypothalamus N.P.O. (Nucleus Prooptics) and N.L.T. (Nucleus Lateralis Tuberalis) which secrete polypeptides that control the function of the pituitary gland, triggering release of pituitary hormones.
3. **Adrenal Medulla**, which responds to a nervous input by releasing adrenalin into the blood stream.

This knowledge of nervous endocrine-co-ordination has laid the foundation of the new science of **neuro-endocrinology**.

Hormones are today the prime weapons in combating over-population (the pill); the genesis of cancer, immunological protection, *etc.*, which have enormous importance for the future welfare of the world. Hormones should no longer be regarded as merely chemical messengers in the blood stream; they play a part in almost every living process.

Chapter IX

INFORMATION (SENSE ORGANS)

All animals find their food, mates, living niches, and avoid enemies and environmental hazards, by a system of special sense organs or **receptors**, gathering requisite information. This information is fed into the Central Nervous System through the peripheral nerves to cause the desired reaction. In all higher animals sense organs or receptors of the body are functionally divisible into two main categories: (A) **Organs of special sense**, limited to the head, such as, for smell, vision and hearing; and (B) **General sensory system**, distributed more or less diffusedly throughout the body, for perceiving pain, touch, pressure, heat, cold *etc.*

Receptors are again locationally divisible into three types: (a) **exteroceptors**, receiving stimuli from the external environment; (b) **interoceptors**, perceiving stimuli from the internal viscera, such as sensations of hunger and thirst; and (c) **proprioceptors**, which are concerned with reception of control stimuli from muscles, joints and other deep part of the body.

Exteroceptors: These are specialised to receive stimuli which may be grouped into three main types: (1) **mechanical**, (2) **chemical** and (3) **radiant**.

Mechanical receptors are of five types: (i) **tangoreceptors** for touch and pressure; (ii) **phonoreceptors** for hearing; (iii) **algosireceptors**, for contact pain; (iv) **electroreceptors**, for perception of electric current; and (v) **rheoreceptors** for orientation in water current.

Chemical receptors are: (i) **olfactoreceptors** for smell; (ii) **gustoreceptors** for taste; and (iii) **irritoreceptors** for chemical irritation.

Radiation (radiant energy) receptors are: (i) **caloreceptors** for heat; (ii) **frigidoreceptors** for cold; and (iii) **photoreceptors** for light.

Interoceptors: These perceive: (i) appetite; (ii) hunger; and (iii) thirst.

Proprioceptors: These are: (i) **myoreceptors** for muscular sense or tonus; (ii) **nocireceptors** for visceral pain sensations; and (iii) **equilibration and orientation receptors**.

A. ORGANS OF SPECIAL SENSE

The main organs of special senses in vertebrates are: **nose** for olfaction, **eyes** for vision and the **ears** for hearing and equilibration.

1. Odour and chemical sense (Olfactoreception)

In invertebrates, insects have possibly the highest sense of smell, *e. g.* male moth finds the female by the characteristic scent emitted by the latter, the olfactory organs being usually situated in the antennae. In grasshoppers and butterflies olfactory organs are present in palps and in some flies in the labella. A special chemical sense is present in some dipterans, bees and beetles, enabling them to detect water vapour and its gradients. This serves them to find water from long distances. Such faint chemical sense is possible due to many odoriferous substances giving a range of wave lengths.

Most carnivorous fishes and mammals are **macrosmatic** (highly sensitive to smell), such as sharks, dogs and big cats. On the other hand **anosmatic** (having no olfactory sense) birds and mammals are known, *e. g.* toothed whales and most birds. (The kiwi is an exception and can follow trails like a dog; this may possibly be due to a non-flying mode of life). Most amphibians,

reptiles, and the primates including man are **microsmatic** (having a little sense of smell).

The smell stimulus is received by the epithelium of the upper part of the nasal cavity and passed through the olfactory nerve into the central nervous system. In land vertebrates only volatile substances or gases can be smelt. In aquatic vertebrates (*e.g.* sharks) the olfactory organs are large, with their surface areas increased by a large number of mucous folds arranged like the leaves of a book. These are called **Schneiderian folds** in fishes. It has only recently been found that olfactoreceptors in the anterior part of nose respond to water soluble substances in the main, while those at the back perceive fat soluble substances.

Olfactoreceptors in mammals are the olfactory hair cells, with their fine hairs projecting above the free surface, which is always kept moist. The Bowman's glands in the nose secrete this solvent which dissolve air borne molecules, thereby facilitating olfaction. In cats and tigers a special vomero-nasal **organ of Jacobson** is highly developed and is an accessory olfaction organ. Being an invagination of oral mucosa, it can smell as well as taste the food, perceiving **flavour**.

The perception of smell is as much dependent on the sensitivity of *olfactoreceptors*, as on the nature of the compounds smelt. For example, a volatile compound, mercaptan, can be smelt by man at a very low concentration of 4×10^{-11} grams/litre; on the other hand many well known substances gives no smell at all.

2. Visual Sense (Photoreception)

The perception of light waves is by special photochemically active carotenoid pigments (easily obtained from carrots), starting from protozoa, such as **Euglena**, **Phacus** and others with an eye spot. In metazoa, the earthworms, for instance, are sensitive to light, possessing definite photoreceptors with transparent lens-like structures for concentrating light. No definite is formed in eye spots or simple photore- The brates to form an image are polycha-

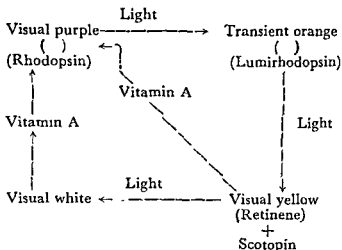
containing **ommatidia** in their compound eyes. Besides, true eyes are found in molluscs and vertebrates.

Light waves initiate in the neurons of photoreceptors, a photochemical reception, which in turn initiates **summation** and **discharge** into the connective nerve fibres. The vertebrate eye is highly sensitive to the photochemical reactions involved and it is claimed that even 5 light quanta may initiate such a discharge.

The eyes of **vertebrates**, in general, respond to a small part of the electromagnetic spectrum, with wave lengths ranging from 380 to 760 millimicra (visual light). The human vision ranges from 397 to 723 $m\mu$ and is most acute at 510 $m\mu$. The infra-red detectors of snakes, with which they find their rodent prey, do not lie in the eyes, but in a separate pit near it. It is sensitive to infra-red rays from 1.5 to 15 μ . In a similar category may be placed the special sense organs of many invertebrate parasites, such as bed bugs, leeches and ticks, which make a beeline for the warm-blooded host. Ultraviolet waves are, on the other hand, perceived by planarians, and the water flea **Daphnia**. A sensation of light is also produced on the retina of man by X-rays.

The main problem of **photoreception** can be underlined under two heads; (i) peripheral mechanism; and (ii) the central mechanism. The initial event in the process of vision is a photochemical reaction in the retinal cells. The mammalian eye contains a rose coloured photochemically active pigment **rhodopsin** (**visual purple**). It is a chromoprotein with a caroteniod as the prosthetic group. Rhodopsin is produced in darkness and breaks down rapidly in light into a yellow pigment **retinine** (**visual yellow or vitamin A aldehyde**) and a protein **scotopin**. If one remains in the dark for some time, rhodopsin is completely regenerated and rods become charged with it; if one goes out into the bright sunlight, the breakdown is so quick that if he returns to a shaded room, he perceives darkness. This breakdown and its products stimulate the nerve endings of the bipolar neurones of the retina.

The photochemical cycle can be expressed as follows :



For the resynthesis of rhodopsin, vitamin A is essential. (Fresh water fishes have another vitamin A, **vitamina A₂**. It takes part in a similar photochemical cycle, the pigment corresponding to rhodopsin being called **porphyropsin**). Vitamin A deficiency results in "**night blindness**" (**nyctalopia**) ; a person suffering from this disease may require hundred times the light intensity as he would with normal eyes. Night blindness is cured by high vitamin A administration (as for aeroplane pilots).

Nocturnal animals can see at night and have strong vision in dimlight. This is due to a special sensitiser layer in the choroid, called *tapetum lucidum*, which also causes eyes to shine in the dark. In addition to *tapetum*, night vision eyes have two other modifications : (a) greater photosensitivity of the retina, due to a large number of rods ; (b) presence of a slit pupil instead of the round pupil of diurnals.

Colour vision : Colour vision and the perception of bright light is due to the cone cells in the retina (Fig. 84), containing another pigment **iodopsin** (rod cells perceive noncoloured and comparatively dim light). Animals such as sharks and primitive fishes, rats and mice, with no cones in the retina, cannot discern colours ; whereas vertebrates from some bony fishes to man have an increasing number of cones in the retina (about 115 million rods and 6.5 million cones in the human eye). The **yellow spot**

(macula lutea), lying to one side of the blind spot, contains only cone cells for acute vision and colour sense. Binocular

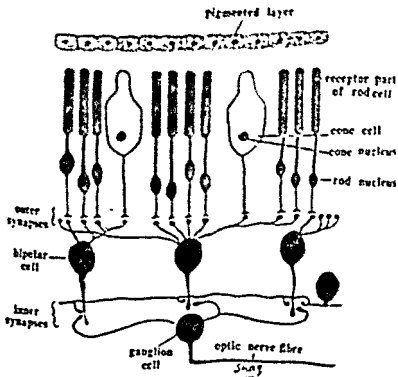


Fig. 81. Cellular structure of the retina in a mammal, showing rods and cones.

stereoscopic vision is obtained in man, monkeys etc., by forming one object in both the eye-retinas.

The sharp vision of the birds eye (eagle watching from a high perch their prey on the ground) is due to : (i) the presence of the extended fovea centralis in retina for acute vision containing only cones; and (ii) presence of a fanlike structure called pecten in the eye, allowing for a quick photochemical cycle.

Colour blindness or deviation of colour vision, specially red-green, is a characteristic human genetic phenomenon occurring only to males, 8% of all males being such colour blind. Colour blinds may be monochromats, in which case no photochemical substance is present; or dichromats, in which case only one photochemical substance is present.

colour blind people) who have two photochemical substances; as against the normal **trichromats**, with normal colour vision and three photochemical substances.

The **visual pathway** (Fig. 85) consists of the chiasma, formed by the discussion of some optic nerve fibres. Fibres

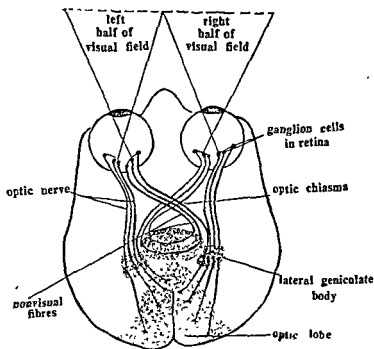


Fig. 85. Route of the optic nerves (the visual pathway).
(After D'Amour)

from the right half of the left eye cross over to continue as the right **optic tract** into the **occipital lobe** of the brain. Similarly fibres from the left half of the right eye, cross over continue as the left optic tract with the fibres from the left side of the left eye. Thus the left side of the occipital lobe perceives the right side of the visual field and the right side of the occipital lobe sees the left visual field. This causes righting of the image formed.

3. Photoreception and Equilibration

Sound is transmitted as waves of compression and depression of various media, and **hearing** is the reception and interpretation of this stimulus.

Among invertebrates sound perception has been studied in grasshoppers, crickets, cicads and some moths. These have an auditory organ in the tibia of each front leg, essentially consisting of sound sensitive cells covered by a thin membrane. Grasshoppers have a sound perception ranging from 430 to 90,000 cycles per second, while some moths can listen upto 80,000 c. p. s. Sound perception in animals is an attracting device for mating, identifying own species and enemies through ultrasonic echolocation.

VERTEBRATE EAR

Sound travels faster in a denser medium (water) and slower in a rare medium (air). Therefore though basically the auditory organs of vertebrates conform and work on the same principles (sound perception by internal ear), higher land vertebrates have evolved supplementary organs for sound amplification, direction and transmission (external and middle ear).

INTERNAL EAR

The essential organ of hearing in all vertebrates is the internal ear, consisting of: (i) **membranous labyrinth** (3 semicircular canals, a utricle, a saccule, and in mammals a spiral cochlea), and (ii) **bony labyrinth** which contains the membranous labyrinth. The space between the two is filled with a fluid **perilymph**, while **endolymph** is present within the membranous labyrinth.

small ducts. The organ of Corti with receptor hair cells lies stretched on a taut **basilar membrane**.

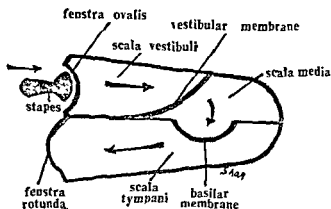


Fig. 86. Transmission of sound in cochlea (inner ear) (diagrammatic) Arrows indicate the path of vibrations

Fishes have no cochlea, but the macula of sacculus can perceive sound. In *Ostariophysi* there is a chain of **Weberian ossicles**, which are the modifications of first four vertebrae. These extend from the sacculus to the air bladder and transmit sound waves amplified by the air bladder.

In **amphibia** the cochlea is absent and is represented by **lagena**, a projection of the sacculus. There is a single bone, **columella auris** in the middle ear for sound transmission.

Reptiles have a small cochlea and one **columella auris**. Snakes have no tympanum at all and the columella is attached to the quadrate. Therefore snakes are deaf to sound waves transmitted in air; however they hear large amplitude sounds which reach them through the ground. Birds have a definite though less developed cochlea.

Hearing (Fig. 87) : The external ear (in mammals) amplifies the sound waves, leading them on the **tympanic membrane** and vibrating it. The induced vibrations of the tympanic membrane are transmitted to the membrane of the **fenestra ovalis** (oval

window), through the ear ossicles, where they cause vibrations of the same frequency. Vibrations of the fenestra ovalis membrane

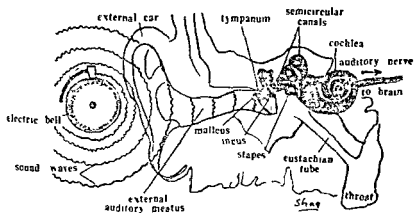


Fig. 87. Diagram to illustrate hearing in man.

cause vibrations in the **perilymph** of **scala vestibuli**, **basilar membrane**, **scala tympani** and **fenestra rotunda** (round window), setting up a vibrating system.

On the basilar membrane rests the hair cells of the **organ of Corti**, which stimulated by vibrations send impulses through the nerve fibres of the **cochlear branch** of **auditory (VIII) nerve**. These impulses are transmitted to the **acoustic area** in the temporal region of cerebral hemispheres, which produce the **sense of hearing**.

Perception range of different vertebrates varies: for man it is from 16 to 20,000 c. p. s.; and most sensitive at 2,000 c. p. s.; for dog upto 30,000 c. p. s.; while bats produce and perceive ultrasonic upto 100,000 c. p. s. Thus bats and dogs hear high pitch sounds inaudible to man.

The ability of vertebrate ear to perceive the **intensity** of sound depends on wave frequency. (Insects on the other hand are more sensitive to sound phase rather than pitch and tone. The **direction** from which sound is coming is determined by the phase difference obtained by the right and left ears, depending on the

distance difference which the sound travels to reach the two ear drums.

The acuity of hearing in mammals possibly depends on the form and number of spiral turns in the cochlea of various mammals. The spiral turns are : platypus, $\frac{1}{2}$; whale, $1\frac{1}{2}$; horse, 2; rabbit, $2\frac{1}{2}$; man $2\frac{3}{4}$; cat and dog, 3 and some small rodents, such as squirrels, rat, and mice, have 5 spiral turns.

Sound has two properties, **loudness** and **intensity**, which are at times confused with each other. Loudness is what is heard as auditory sensation, while intensity is a physical term expressing the energy or physical power of the sound waves. Intensity of sound is expressed in **decibels** (a decibel being one tenth of bel which is the logarithm of the intensity of sound as compared to a sound which can be just heard). The rustling of leaves in a breeze has an intensity of 10 decibels and a loud peal of thunder, 70.

It has been established that the intensity of sound affects a man adversely, if it is above 100 decibels. Above 150 men become restless and cannot concentrate. Sounds above 200 decibels in a confined space will turn most men insane within some hours. Exposure to constant high intensity sounds produced by the everyday activities of modern civilised man has been termed *noise pollution*. It is a serious problem in the industrial cities and towns of the world. Efforts are being made by U. N., UNESCO and other organisations to reduce, if not eliminate noise pollution which affects the health, mentality, longevity etc. of modern man, exactly as air and water pollution does. On the other hand a low decibel music has been found to affect man, cattle and milch animals, beneficially. The man relaxes, cattle fatten and milch cattle yield more milk.

Echolocation in Bats (Fig. 88): Small bats (microchiroptera) have been found to emit short bursts of ultrasonic sound waves (inaudible to human ear), upto 100,000 c. p. s. The reflection or echo of these waves give them the location of solid objects in their path, such as obstacles and prey. A bat can avoid a maze of strings, stretched across a room, even after being blinded. The incident sound is generated by vocal cords and reflected waves received by ears.

EQUILIBRATION

In most invertebrates studied, the reception of sound waves and the process of maintaining equilibrium are not functionally

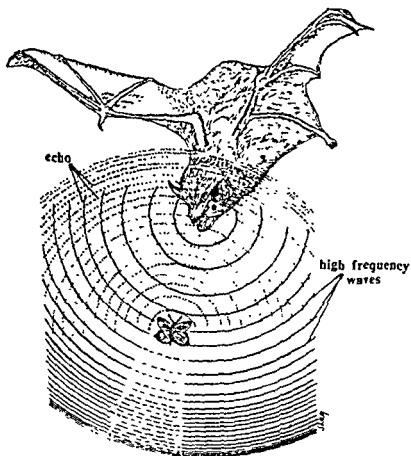


Fig. 88. Echolocation in bats (the insect is located by means of reflected sound waves (dotted curves) (After Griffin)

connected. But in vertebrates the two functions are mainly carried out by ears which may be called **Stato-acoustic organs**.

Some protozoa react to gravity, *e. g.* **Paramecium** positively and **Euglena** negatively, and perhaps possess some sort of **georeceptors**. Coelenterates and most arthropods have **statocysts** for maintenance of a constant position with respect to earth's gravity.

Essentially, these are hollow chambers with sensory receptor cells on their inner surface. The chambers contain sand or calcium carbonate grains (secreted or obtained from outside). These grains called **statoliths** are comparatively heavier than the surrounding medium. When these grains come into contact with sensory cells by a change in position, the nerve endings are stimulated. These start reflexes causing the animal to orientate itself with regard to the force of gravity.

If the statocysts of a jelly fish are damaged, the animal is no longer able to right itself and floats in an upside down position. A moulting prawn if provided with iron powder instead of sand incorporates these into statocysts. It can then be forced to swim in any position by the manoeuvrings of a magnet.

Semicircular canals with their ampullae are the main organs of equilibration in vertebrates. These canals are placed at right angles to each other in three planes. Hag-fishes have only one semicircular canal and lampreys two. They have thus got *one plane* and *two plane ears*, perceiving one dimension and two dimensions respectively, as compared to the *three plane ear* of other vertebrates, sensitive to three dimensions. Patches of delicate hairy receptor cells supplied by the vestibular branch of auditory nerve perceive stimuli caused by any movement of the endolymph. Each sensory patch is termed **crista ampullaris**. Calcium salt concretions, called **otoconia** or grains are present, attached to the receptor cells, particularly in land vertebrates. They have a function similar to those of invertebrate statocysts. As the three semicircular canals are in three different planes, the combined stimuli received by the ampullae allow detection of any positional shift.

In order to prevent the upsetting of this highly sensitive apparatus by ordinary small body movements, semicircular canals are lodged deep in the temporal bone. However, equilibration mechanism is not solely dependent on semicircular canals alone. Eyes, pressure receptors and proprioceptors also contribute to the maintenance of equilibrium and orientation.

B. GENERAL SENSORY SYSTEM

Taste (Gustoreception): The sense of taste possibly originated as a reaction to chemical stimuli, such as the positive response of *Amoeba* to food or weak acid; reaction of tentacles of sea anemone to proteins; Jelly fish response to lipids, fats *etc.* These can be termed general taste responses. However, in invertebrates, definite taste organs appear first in the insects, *e.g.* the Cockroach on the labial and maxillary palps; the bees and wasps on the antennae, butterflies and flies in general on the tarsi of legs (leg taste). Experiments have shown that insects can distinguish between acid, alkali, salt, sweet sugar and bitter quinine.

In the lower vertebrates, fishes, frogs and toads appear to be poor in taste, although copious taste buds are present in some fishes, such as loaches and catfishes, on barbels. The tongue of frogs and toads responds to only salts and acid. In the higher vertebrates taste buds (Fig. 89); are highly organised on the specialised tongue and buccal cavity. The taste buds in human tongue

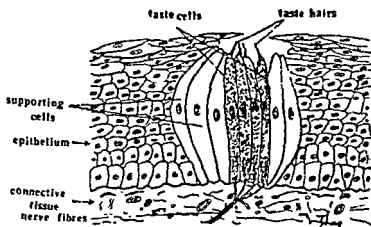


Fig. 89. A taste bud in section showing taste cells with taste hairs.

are distributed in four primary taste areas, for the tastes of sweet, sour, bitter and salty. A sense of sweetness is sharply localised at the tip of the tongue, saltiness along margins; bitterness on the posterior region and sourness chiefly along the edges. Taste or gustation is the perception of dissolved materials, by, taste buds,

Many tastes are not tastes at all, but a sense of touch, temperature and pain, such as the bite of the ginger, the pepperiness of pepper and heat of chillies. Others again are not tastes but smell, which can be seen in a man suffering from acute cold, to whom nearly everything is tasteless.

Some tastes cannot be sensed at all by some people, *e. g.* solution of one in 100 thousand phenyl-thiocarbamide (a harmless substance) which tastes bitter to most people is tasteless for others. In experiments 65.5% people reported the substance bitter; 28% tasteless; 2.3% sour; and 4.2% some other taste.

The nerve fibres for taste from the anterior two thirds of the tongue pass into the VII (facial) cranial nerve; those from the posterior third go into the IXth nerve (Glossopharyngeal). There is a salivary reflex, for which the sense of taste is the chief sensory component.

Pain (algosireception)

Pain is felt through definite, specialised free nerve endings called **algosireceptors**. Pain is caused by excessive stimulation of the nerve endings by too brilliant light, high intensity sound, contact with acute cold, scalding heat, acute pressure *etc.* These pain impulses are perceived more acutely by massed free nerve-endings, the **nocireceptors**, concerned with injuries (Fig. 90). In large number of invertebrates the skin is protected by chitin, cuticle, shell *etc.*, which reduce the chances of warning pain, and thus algosireception in these skins is poor. Similarly, fishes and reptiles with protective scales have also less algosireceptors.

In higher vertebrates numerous algosireceptors are present on external skin and other exposed parts of the body. The pain impulses can be perceived by the entire C.N.S., there being specific areas in the brain for pain responses alone (as also for touch, pressure, heat and cold), similar to ones which exist for sight, hearing, smell and taste.

Touch (Tangoreception)

Tangoreceptors are of two kinds: (a) thigmoreceptors or tactile receptors; and (b) pressure receptors.

Tactile receptors are common in the tentacles of coelenterates, skin and tentacles of annelids, antennae of arthropods *etc.* In vertebrates tactile receptors occur extensively on most parts of the skin, being closely spaced on the face, palm or surface of hands

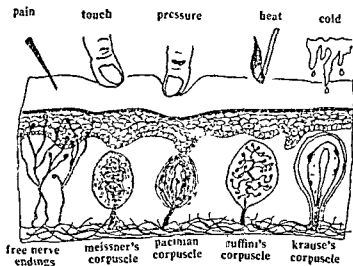


Fig. 90. Diagrammatic representation of the skin-receptors for pain of touch, pressure, heat and cold.

and feet and tips of the fingers. This distribution can be felt by touching a finger tip at two points, only 0.23 cms apart, giving separate sensations of touch in man; whereas on the back of the body we can feel separate touch sensation only at and beyond 6.7 cms. If the distance between two touch points is less than 6.7 cms only one touch sensation is produced. The touch receptors are special **Meissner's Corpuscles** (Fig. 90) in the dermis, supplied by nerve endings.

When touch is sustained beyond temporary contact, it is interpreted as pressure. Pressure is sensed though specialised **Pacinian Corpuscles** (Fig. 90) in the skin. These are located more abundantly in places where they usually come into contact with external objects. Thus the knee in man is more sensitive to pressure than the thigh; the friction areas of hands and feet much more than the scalp; and the concave surface of the prehensile tail

of Chameleon and Langoor monkey more than the convex surface.

Pacinian corpuscles are present in the **labia majora** of females, for pressure. Besides these special end bulbs (Fig. 91);

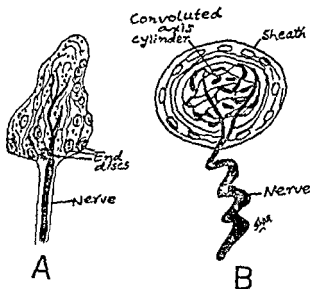


Fig. 91. Sensory end bulbs for pressure :
 A—From human clitoris
 B—From human glans penis.
 (After Das)

for pressure and extra-sensation are abundantly found on the **clitoris** in female and **glans penis** in male, stimulating orgasm and ejaculation respectively.

In some fishes the barbels around the mouth contain numerous thigmoreceptors, as for example in catfishes and loaches. Amphibia have touch receptors on mucous membrane of the tongue as well as the skin. Reptiles have a highly tactile tongue, which in snakes is seen as protrusible, forked and continuously flickering in and out of the mouth. In general tangoreceptors are absent in the scaly skin of fishes and reptiles. These are more abundant on the base of *vibrissae*, with which burrowing and arboreal animals move with ease.

Heat and Cold (Thermoreception)

There are two types of thermoreceptors, viz. *Caloreceptors* for heat and *frigidoreceptors* for cold. *Ruffini's corpuscles* (Fig. 90) are responsible for heat perception. They lie deeper in the skin and are less numerous than the cold receptors. Hot temperature is registered by the *caloreceptors*, but at a lower point they handover the reception to *frigidoreceptors* for cold. Frigidoreception is by specialised *Krause's corpuscles* (Fig. 90), which lie interpersed between the less numerous *caloreceptors*.

Caloreceptors are practically absent from the front of eyeballs and are abundant on the face, hands and feet. The hot or cold effect is dependent upon the number of receptors involved. The total effect of warmth or cold, for example is different if an exploratory finger is plunged in hot or cold water, than if the whole hand is submerged at once. It is peculiar that the *calo-* and *frigidoreceptors* are so specialised that even if a hot needle is placed on a *frigidoreceptor* area, it will produce a sensation of cold and if a cold needle is placed on a *caloreceptor*, it will produce a sensation of heat.

It has been estimated by mapping of certain cutaneous regions that in the entire skin of a normal human adult, there are present 4 million *algosireceptors*, 5 hundred thousand *tangoreceptors*, 5 hundred thousand *thigmoreceptors*, 30 thousand *caloreceptors* and 250 thousand *frigidoreceptors*. *Algosireceptors* therefore outnumber all the other receptors of the general sensory system. If this were not so, animals would hardly be able to live, not capable of perceiving avoiding or overcoming the different environmental hazards, for pain is a protective reaction in animals from amoeba to man.

Current perception (Rheoreception): Rheoreceptors are entirely absent in land invertebrates. But four general kinds are recognizable in fishes and aquatic amphibia: (1) Lateral line organs (2) Scattered pit organs, (3) Ampullae of Lorenzini and (4) Vesicles of Savi.

Lateral line organs are found in cyclostomes, sharks and rays,

most bony fishes and in some amphibia. The functional receptors in the lateral line and special neuromast organs arranged in a line sunk in the skin, on each side of the body, each made up of cells with sensory hairs embedded in a gelatinous matrix—the **cupula** (Fig. 92). These are not able to receive current stimuli, but also pressure of the water column above it and water pressure against solid objects at a distance. They can therefore be termed as *distant touch receptors*.

The **pit organs** are isolated neuromasts sunk in the skin in separate pits, in some fishes. Agitation of the water of pressure perception is their chief function.

Ampullae of Lorenzini are found abundantly in the skin of the head and snout of cartilaginous fishes. Each ampulla consists of a group of sensory cells and a tube with an external opening containing sensory hair. Their function is to perceive pressure and rheoreception. **Vesicles of Savi** are abundant in flat fishes such as Torpedo.

With the help of all these receptors, fishes are enabled to steer in water currents, even in darkness or in turbid waters, when no landmarks are visible and this maintain their position by swimming against the current or in some cases away with the flowing tide or current. They also help by distant touch in making a fish aware of approaching enemies, large prey and obstacles in their path.

Interoception

Appetite, hunger and thirst are sensations associated with interoceptors in the digestive system. No distinct receptor organs have yet been demonstrated for interoception. Appetite, hunger and thirst are the three-primary sensations caused by interoceptors. Appetite is a pleasant sensation brought about by internal changes and reflexes, as a result of such external stimuli as sight, odour, or taste of food. Hunger, is an unpleasant sensation often confused with appetite. It is the result of nutritional poverty in blood affecting interoceptors in the circulatory systems, and not

due to muscular contractions of an empty stomach as usually supposed. Thirst is also an unpleasant sensation, due to increase

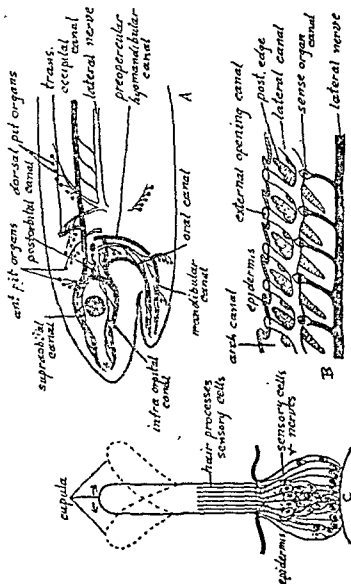


Fig. 91. General distribution of lateral line neuromast organs, and canals with their nerve supply.
 B—Lateral line canal in trunk region of teleost fish.
 C—Neuromast organ with cupula of teleostfish.

in osmotic pressure (Salt content of the blood) this compels the animal to replace the lack of water in blood and the tissues of the body. Thirst is not due to the mucous lining of the throat. The entire body cries out for water.

Proprioception

These are definite sense organs closely related to pressure of one sort or the other, through muscles, Tendons, joints, position of the different parts of the body *etc.*

These do not produce well defined sensation, but are concerned with the so-called general kinesthetic sense. Proprioception can be seen in mechanisms of complicated acts, such as walking, skating, cycling, typing. It is primarily responsible for the feeling of posture and equilibrium in all vertebrates. In somnambulation (sleep walking) the man balances and walks with his eyes closed without falling, with the help of proprioceptors.

Proprioceptors are therefore myoreceptors and nocireceptors, equilibration and orientation receptors.

Chapter X

REPRODUCTION

Reproduction, in its broadest sense is the survival of the species rather than the individual. A definition is difficult but a close one would be the production of an animal or plant which is in some way a different individual from the parent or parents which gave rise to it. Reproduction in animals can be classified into **asexual** and **sexual**. Asexual reproduction is commoner in the lowest animals *e.g.* Protozoa, Porifera and Coelenterata, although a vast majority of them also show sexual reproduction.

ASEXUAL REPRODUCTION

Asexual reproduction is wide spread in protozoa and occurs by three mechanisms (a) binary fission, in which the two daughter cells are equal in size, the plane of division being transverse (Amoeba, Paramecium), longitudinal (Euglena, Vorticella); and oblique (Opalina), (b) Multiple fission as seen in sporogony and schizogony in sporozoa (Plasmodiums) and (c) Budding, common in many Protozoa, *e.g.* Vorticella (specially in Suctorina

or more cells float together and fuse (compound larvae of sponges).

In the ciliates binary
reproduction of the parent
reproduction and growth.

redifferentiation occur in metaxoan regeneration of amputated parts, while many Ectoprocta and Tunicata become dedifferentiated, with reduced bodies under adverse conditions, and under-reconstitution (restitution).

~~Here~~ Sponges and hydroids also have a remarkable capacity of reconstitution of separated parts which reaggregate and produce a functional organism. Against this many simple metazoans as *Hydra*, *Aurelia*, *sea-anemone*, *(Chaetogaster)* have

example *Hydra Schyphostoma* or *Aurelia*, divide transversely, on the other hand sea-anemones divide longitudinally.

In *Convoluta*, fragmentation appears to be the normal method of reproduction, as also some fresh water oligochaeta (*Naias*, *Elosoma* etc.). Here division takes place at a definite fission zone; where several new segments are interpolated and reconstituted, only after which fission takes place. The axial gradients (first demonstrated by child are so arranged that even if a chain of many parts is formed as in *Naias* it swims about as one individual until just before separation. In many Polychaetes there is regular asexual reproduction by spontaneous fragmentation into short lengths, the anterior end of each fragment forming a head. The syllid polychaetes fission and separate to form sexual individuals (*Syllis remosa*) Corals grow rapidly sometimes as huge colonies by repeated longitudinal fission of polyps which however remain attached and secrete new skeleton.

In sponges budding is a specialised one, by gemination. This is almost like vegetative reproduction in plants except that the gemmae may remain attached and result in huge sponges. However in adverse conditions, the gemmae separate, form hard cysts called gemmules *Hydra* is specially amenable to budding and

male and female gametes are produced by the same individual. In most however, cross fertilization is usual due to **protandry** (male gametes maturing earlier e. g. *Oysters* and *Herdmania*) or **Protogyny** (female gametes maturing first) in cyclostome, *Myxine* and species of *sparoidea* and *serranidae* are invariably hermaphroditic amongst fishes, *Myxine* being protandrous. The eggs and sperms are produced in different areas of the same gonad without self fertilization being obligatory except in the cyprinodont *Rivulus* which is a self fertilizing hermaphrodite. The eggs of *Rivulus* are usually fertilized in the oviducts of *Polychaeta* and *Echinoderms* and *trematodes* leeches although have cross fertilization with formation of egg cocoons. The arthropods and molluscs have copulation and fertilization before the egg is deposited in the vertebrates unisexual.

Sex Reversal: Although maleness and femaleness are characteristic of sexual differentiation in unisexual animals, strange cases

old hen becoming a cock, and a boy turning into a girl (in the toad the male regularly turns later into a female the Bidders organ at the anterior end of testis acting as a rudimentary ovary).

Bonellia, in which the female is 1 mm long. Here the young which live away and free from female adults develop usually into complete females. But in some cases they develop into males. This is probably a final

family *Calyptraeidae* are examples of consecutive hermaphrodite animals; the young are small males which remain attached to a female with their long copulatory Phallus reaching the seminal receptacles of the much larger female. This is followed by a transitional stage in which the animal grows in size and undergoes sex reversal. The Phallus becomes absorbed, female genital ducts

fertilization) the allator lives the interior of the Porous Calcareous shell, acting as a respiratory organ. For nutrition of the

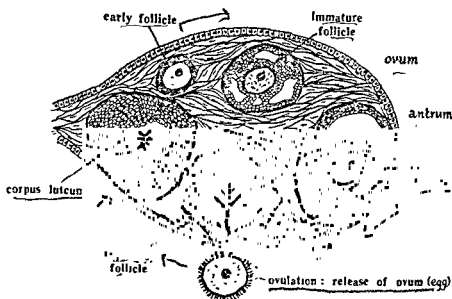


Fig. 93. Stages in the development of Graafian follicle and ova in mammals

embryo the egg (which is a single cell, the largest such animal cell being the egg of the Ostrich) contains white yolk, yellow yolk and albumin.

In mammals a layer of follicular cells surround the ovum (Graafian follicle) inside which are the Vitelline membrane and the zona pellucida. At ovulation, the Graafian follicle ruptures and its walls become folded and vascular to form an endocrine organ, the corpus luteum (Fig. 93); which secretes the important hormone Progesterone. The follicle cells themselves secrete the follicular hormone called Oestrone.

The mammalian ovary has the functions of :

- (1) egg production (Fig. 95);
- (2) elaboration of follicular hormone oestrone;
- (3) production of a luteal hormone progesterone;

- (4) ovulation, often conditioned by coitus, and stimulation of female organ;
- (5) housing and nourishing of developing young (follicular gestation; intraovarian in *Gumubusia* fish; and
- (6) the ovary also acts as a food store, since there is follicular atrecia (as in most fishes, in which mature ova are resorbed as food).

The ovarian hormones control : (a) the secondary female sex characters, (b) the development and maintenance of accessory reproductive organs; (c) the Oestrous and menstrual cycle; and (d) internal changes in mammary glands, pelvic bones, uterus, cervix etc. (Fig. 94).

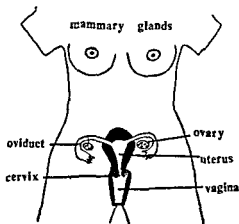


Fig. 94. Production of ovarian hormones and accessory reproductive organs, and also secondary sex characters.

The Sperm and the Testes

Symptomen

Spermatozoa, are formed from the germinal epithelium of the testes, each consisting of a head, neck and a tail (Fig. 95) (the crustacean and echinoderm sperms however have a large head and three eggs. This is released by the sperms. Their activity is due to certain phospholipids which

breakdown giving them the energy for locomotion. A spermatozoan is a minute fraction of the egg in volume in man the ratio

asphatolysis

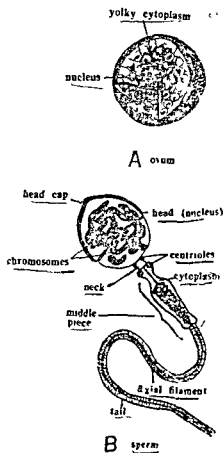


Fig. 95. The sex cells in humans :
A—Ovum
B—Sperm

is about 1 : 195 thousand, but some fishes (cod fish) may produce up to thousand. In invertebrates six million eggs per year.

Testes: Testes may be compact (cockroach) or tubular (nematodes). In the vertebrates testes elasmobranchs have ampullary testes and in the higher vertebrates testes are empact structures formed of lobules, each lobule containing convoluted seminiferous tubules in mammals.

Androgen: Producing endocrine tissue has been recorded in the testes of all vertebrate animals. They are of three types:—

- (a) Interstitial cells;
- (b) cells of Leydig, and
- (c) lobule boundary cells in the walls of seminiferous tubules (specially in fishes).

The testicular hormones control: (a) stimulation for maleness; (b) development of accessory reproductive organs (Fig. 97);

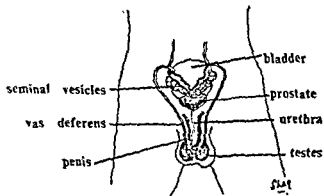


Fig. 97. The fully developed male reproductive organs in man controlled by testicular hormones.

and (c) conformation of the male body; stimulation of the male organs.

REPRODUCTIVE RHYTHMS AND BREEDING SEASONS

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Palolo worm of Atlantic) exhibits a remarkable rhythm conforms

to lunar rhythm. These worms swarm during a limited period, from the last quarter of June to July monsoon: During this time tails of the worms separate which from the main tubiculous body i. e. the tails constituting the swarms liberate gametes before they die. Some molluscs and sea urchins also exhibit a similar spawning lunar periodicity.

Most vertebrates exhibit regular breeding seasons. Birds are very sensitive to seasonal and light periods. Their testes are subject to great seasonal variation, enlarging in size, in the breeding season (usually non-breeding season) is due to Light effect through the optic, Hypophysectomy may result in resorption of the eggs:

- (1) Fishes show a remarkable breeding season by light and temperature;
- (2) Frogs may be induced to spawn by artificial light, even in December; and
- (3) Birds and Reptiles have a seasonal reproduction and many snakes have been found to have an annual cycle of many enlargements of testes and spermatogenesis.

Reproductive rhythm is still more important in mammals, in which both at the same time. all marked in the e. Ovulation in almost all mammals occurs during the period shortly before or shortly after birth (exceptions are the armidallo and a few lower Primates). Surprisingly oesterus occurs only after copulation. In some mammals tion occurs about ten hours af these is at the top of the fallopian it is usually in the lower part. The simplest sexual rhythm in mam- mals during only one season of the year se- occurs during spring. However ti- tivora, Carnivora, Rodentia and n

breed in April in the northern hemisphere and September in the southern. In most artiodactyla, however the rutting season is in autumn and the young are born in spring, since they have a long gestation period. In the weeds small carnivores and bats there is delayed implantation due to blastocyst remaining dormant in the first two cases and due to sperms being stored after copulation in bats until fertilization in spring. Although Oesterus cycle fits in with the annual breeding cycle it may not necessarily synchronise. There are few phases of the oestrous cycle: (a) monoesterus—one ovarian cycle in breeding season (most fishes); (b) dioesterus, quiescent period is present between two sexual activity phases, e. g. dogs, cats; and (c) Polyoesterus which have several breeding cycles fitting in one year e. g. rats, mice, rabbits etc. If there is long period of quiescence it is called anoesterus.

Physiological changes in Oesterus: These are:

- (a) degeneration of epithelium of uterus;
- (b) increase in blood circulation and hypertrophy in external genitalia;
- (c) enlargement and cornification of vagina and uterus;
- (d) development of mammary glands; and
- (e) ripening of graffian follicles.

Extracts of ovaries as also urine in both males and females in oesterus, when injected into mice induce oesterus within two days. These Oesterogenic substances identified are, oesterone, oestriol, oestrodial, equiline and Equilenin (all closely related to sterols). While all mammals are dependent for oesterus in some way on light, the strange stimulus of full moonlight has hardly been explained. The Malayan forest rat and most cats have increased oestral activity during full moon periods. Domesticated mammals, such as cow, dog etc., may breed at any time of the year, since excess of food has disturbed the cycle. In monkeys and man the

tion, elimination of

Copulation The mechanism which brings the opposite gametes into contact with each other must be quite reliable. Particularly in land animals in some groups there is no definite organ for the transmission of sperms, however, in some a special organ for this purpose is present. Some snails have a highly muscular penis. The male spider sheds semen on to a leaf, which he applies to the end of his palp. This palp is then inserted into the genital opening of the female. Octopus has a specially modified tentacle called hacto cotylus for this purpose. In male sharks claspers are present for copulation (Chimaeras have a frontal clasper in addition).

Amplexus

During copulation the male introduces sperms into the vagina of the female, a process consisting of two phases: erection and ejaculation, accompanied by contractions of uterus, vagina and cervix in the female to ensure entry of sperms and fertilisation.

Fertilization: (Fig. 98.) It consists of three stages: (a) convergence of numerous spermatozoa to the egg and attachment on its surface, (b) intrusion of usually one sperm head into the ovum with fusion of sperm and egg nuclei. The sperm bores its way in all uronid is no birds. comes impermeable to the other spermatozoa. It is interesting to note

that the first sperms coming into contact with corona radiata in mammals die, and release hyaluronidase which effects liquification of the jelly and dissolution of the cells of corona radiata.

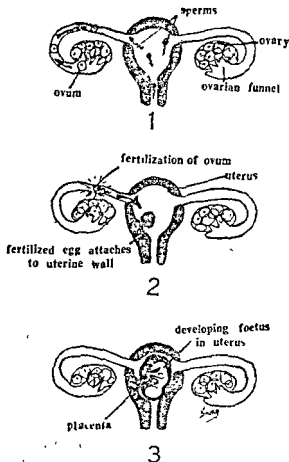


Fig. 98. Fertilisation of egg and formation of foetus (embryo + placenta) in mammals.

- (1) Fertilisation.
- (2) Implantation.
- (3) Placentation.

Recently two types of sperms have been identified in man, the larger and fewer gynospersms, resulting in female embryo and the smaller more numerous androsperms, producing male embryos.

Implantation (Mammalian) (Fig. 98, 2)

After fertilisation and implantation in the uterine wall, the gastrula knob in the trophoblast sends out cells of Rauber, which finally disintegrate, and the embryonal knob is converted into an embryonal disc. The blastocyst becomes greatly enlarged and the zona radiata stretches and finally dissolves away. The trophoblast itself forms a part of the foetal membranes called the chorion. The nutrition of the embryo is ensured by the trophoblastic responding uterine crypts in the uterine wall. This then forms the foetus consisting of (a) Chorion, (b) the amnion, (c) the allantois, (d) the yolke sac, and (e) the embryo.

The embryo lies in a watery fluid enclosed by the foetal membranes, exactly like an aquatic larva living in a pond of its own, inside the mothers body. This is an evidence for the aquatic ancestry of mammals.

Mammalian Placenta (Fig. 98, 3).

placenta

... .. structural connexions
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tion of the developing embryo.

The first food for the embryo is provided by uterine secretions which are absorbed by the swelling blastocyst in the cavity of the uterus. (The embryo is connected to the chorion by the allantois and amnion and is

to the uterine connective tissue and lastly to the walls of the maternal blood capillaries, which are broken down. The result is that maternal blood circulates not only in the uterine lacunae thus formed, but also in the lacunae of the thickened trophoblastic villi. However there is no direct communication between the foetal and maternal blood streams, exchange of substance being exclusively due to selective diffusion through the walls of the foetal and maternal capillaries.

Placental Hormones: Besides the action of gonadotropic hormones from the pituitary, and ovarian hormones from the

mare. They are both glycoproteins, which appear similar to s are somewhat different.

HCG of pregnancy. Its action is similar to that of L. H. (from the pituitary). P. M. S. on the other hand, is of uterine origin, and has an action similar to F. S. H. plus L. H. Unlike HCG it is not excreted, but remains in the blood.

Another hormone **Relaxin** has been isolated from placenta as well as ovaries of several mammals, the action of which is remarkable: (a) it splits and softens collagenous fibres and associated

Reproduction is so highly linked with endocrinology today that both of them have been combined into reproductive biology, which has reached a point where it can be confidently stated that reproductive processes are integrated on similar lines throughout all vertebrate classes, from cyclostomes to mammals including

man. This reproductive cycle is controlled by neurosecretory centres in the brain, which in turn trigger off release of gonado-

hundred million years ago. The
fishes, is a classical example o

as well.

Chapter XI

A SHORT HISTORY OF PHYSIOLOGY

1. Movement

The difference between voluntary and involuntary muscles was first realised by **Galen** as early A. D, 130-200. He also understood the opposite action of antagonistic muscles. By experiments **Galen** was able to demonstrate the intimate relationship of a motor nerve to a muscle i. e. a muscle was paralysed by cutting off its motor nerve.

The microscopic structure of muscle fibre was first described by **Stensen** in 1664 and later more fully by **Leeuwenhock** (1715). **Jan Swammerdam** who used frogs muscle-nerve preparations in his experiments concluded that the volume of a muscle remains constant in contraction as well as relaxation.

Most of the knowledge about muscle action was obtained from 1835 to 1880. **Berzelius** discovered in 1841 lactic acid formation in muscles. Time factor in muscle contraction was worked out by **Helmholtz** in 1850. All or none principle of muscle contraction was demonstrated for the first time by **Keith Lucas** in 1909. ATP in muscles was found by **Lohmann** in 1929. **Gopfert** and **Schaefer** in 1938 discovered the endplate potential.

2. Nutrition

The similarity between digestion of foods in the body and alcoholic fermentation first occurred to **Van Helmont** (1577-1664), though the exact mechanism of enzyme action was not perceived by him. **Stensen** (1662) and later **Sylvius** (1663) elaborated this view of chemical action of digestive juices on food. Pancreatic

juice was obtained by **De Graaf** in 1664, although its functions were not known. In 1752 **Reaumur** studied the action of gastric juice on food substances by a novel method. He induced his tame kite to swallow sponges (which are indigestible) and later regurgitate them, soaked with gastric juice. Reaumur placed bits of various food stuffs in so obtained gastric juice and observed the changes. He concluded that certain ferments (enzymes) were present in the gastric juice which softened and disintegrated food stuffs.

HCl was first identified in the stomach by **Prout** in 1823.

Classical work on gastric secretions and digestion was done by an American military surgeon **William Beaumont** (1833).

Alexis st. Martin, a Canadian was shot through the stomach. **Beaumont** who attended on him expected his patient's death within twenty minutes. However, Alexis escaped death miraculously (and as a matter of fact out lived the surgeon by many years). But the hole of his stomach did not heal. Through this stomach opening Beaumont made various observations regarding the secretion of gastric juice, the state of empty stomach, its movements and the time taken to digest various types of foods. He would tie a piece of meat to an object and withdraw it periodically to see how far digestion had proceeded. Later, artificial gastric fistulae were made in animals, the technique being improved by the famous Russian physiologist **Pavlov** (1898).

Secretin was discovered by **Bayliss** and **Starling** in 1902 while studying the effect of introduction of dilute HCl in the duodenum (which resulted in the secretion of pancreatic juice). The idea of phosphorylation in absorption was put forth by **Verzar** in 1936, while active transport of digested food through the intestinal mucosa had been established by the fifties of this century. Vitamins as accessory food stuffs, were recognized in the late nineteenth and early twentieth century. The name "Vitamin" was originated by **Funk** in 1911.

3. Metabolism

Detailed metabolism of a host of substances became known

with the rapid development of biochemistry in the recent past. **Knoop** (1910) found the oxidation products of amino-acids. Although connection between diabetes and pancreas was established as early as 1889 by **Mering** and **Minkowski**, insulin was extracted and isolated from pancreas by **Banting** and **Best** in 1922.

Anaerobic oxidation by dehydrogenases was discovered in 1920 by **Wieland** and **Thunberg**. Tricarboxylic acid cycle was established by **Krebs** (after whom it is named) in 1940.

4. Respiration

Galen (A. D. 170) had a vague notion of the exchange of gases—addition of something to blood called “vital spirit” and removal of “fuliginous vapours”. **De Vinci** (A. D. 1500) recognized the similarity between burning and breathing. Aeration of blood in lungs was discovered by **Lower** in 1669. **Lavoisier** between 1775 and 1794, outlined the nature of respiration, found the changes of air caused by respiration and determined the oxygen usage of men at rest and work. **Magnus** (1837) analysed the blood gases and demonstrated the difference between arterial and venous blood. **Hoppe-seyler** in 1862 found the haemoglobin—oxygen combination. **Haemoglobin** in blood was described by him in 1866. **Bohr** (1885) put forth the oxygen dissociation curve. Transport of CO_2 in blood was explained by **Hamburger** in 1892.

That the oxygen intake is effected as a result of a difference in partial pressures was established by **Krogh** in 1908

Medullary respiratory centre was first established as far back as 1811 by **Legallois**. Self regulatory mechanism of respiration (Hering-Breuer Reflex) was demonstrated by **Hering** and **Breuer** in 1868. Regulation of respiration by CO_2 was established by **J. S. Haldane** in 1905. Pneumotoxic centre was located and named by **Lumsden** in 1923.

5. Blood and Lymph

Blood: **Leeuwenhock** (1674) was the first man to describe the structure of R. B. Cs. The first haemocytometer was devised

by **Growers** (1877). **Hammarsten** (1176) studied blood coagulation and showed that precursor of fibrin was fibrinogen. Existence of prothrombin and its change into thrombin by calcium salts was established by **Pekelharing** in 1891. Heparin was discovered by **Howell** in 1928.

Landstener (1901) classified blood into groups by discovering their compatibility. (Agglutinin, agglutinin and Rh factor). With this classification blood transfusion became practicable.

Antigen—antibody reaction was however, put to good use by **Jenner** in late 1700 when he immunised people against small pox by introducing artificial small pox virus (against the resentment of church). Napoleon had his entire army vaccinated.

Lymph: Lacteals were described by **Aselli** in 1622. General lymphatic system was discovered by **Bartholin** (1653). **Starling** (1894) contributed to most of the present knowledge about lymph.

6. Circulation

Pulmonary circulation was established as far back as 12th century by Ibn Nafis. William Harvey (1628) first discovered the general circulation of blood in the body. **Malpighi** (1661) discovered the capillaries. **Laennec** (a physician in Napoleon's army) invented stethoscope in 1819.

Much of the work regarding the properties of heart muscles was carried out on frog's heart by Harvey. **Haller** (1736) put forth the myogenic theory of the heart beat origin, whereas **Legallois** (1812) gave the neurogenic explanation for it.

Waber brothers in 1845 showed the inhibitory influence of vagus; while the effect of sympathetic was demonstrated by **Bezold** (1862). First successful human heart transplant was performed in late sixties by **Chris Bernard**.

7. Excretion

That the formation of urine is associated with kidneys was known from very early times. Urea as a constituent of urine was

discovered by **Cruickshank** in 1797; it was the first organic substance prepared synthetically, by **Wobler** (1828). The first quantitative analysis of urine was made by **Berzelius** in 1809. Uric acid was isolated from human urine by **Scheele** and **Bergmann** in 1776.

Bowman in 1842 established the structural relationship between uriniferous tubule, glomerulus and the capsule, discovered independently by **Bellini** (1662). **Malpighi** (1665) and **Muller** (1830) respectively. Filtration-reabsorption theory was first promulgated by **Ludwig** (1844) and later corroborated by **Cushny** (1917). **Richards** (1925) and **Marshall** (1928) studied the kidney of frog and fishes respectively demonstrating active secretion by the kidney tubules.

8. Nervous System

The bases of the anatomy of nervous system were laid by **Willis** (1659) and **Stensen** (1662). **Haller** (1757) described the function of perception and communications of sensations to nerves. The electric nature of nerve impulse was first established by **Galvani** (1786). Axon was discovered by **Wagner** (1851) and the theory of neurone as a functional unit of nervous system was put forth by **Waldeyer** (1891). The conception of synapse is mainly due to **Foster** and **Sherrington** (1897).

The identification of various centres in the brains was carried throughout the 19th century. The velocity of a nerve impulse in frog was determined by **Helmholtz** (1850). Work on the sympathetic and parasympathetic part of the nervous system was carried out by **Gaskell** (1885). Most of the modern work on reflex actions was initiated by **Pavlov** (1903).

9. Hormones

Most of the present day knowledge about endocrine glands and secretion has been obtained in the past 100 years. The term *hormone* was first used by **Bayliss** and **Starling** (1905); they also discovered the first hormone, secretin.

Adrenalin was the first hormone to be isolated and synthesized by **Stolz** (1907).

Insulin was extracted and isolated by **Banting** and **Best** in 1922. Thyroxin was isolated by **Kendall** in 1914 and synthesized by **Harington** and **Barger** in 1927. Parathormone which regulates blood calcium level was extracted by **Collip** in 1929. The important action of pituitary was demonstrated in 1935, when **Evans** extracted growth stimulating hormone. Oxytocin was synthesized by **Du Vigneaud** in 1953. Female hormones were isolated and identified by **Allen** and **Doisy** in 1923. The first male hormone androsterone was isolated by **Butenandt** in 1931.

10. Reproduction

Graafian follicles were discovered by **Degraaf** in 1672 and the ovum first seen by **Baer** in 1827. Sperms were discovered by **Ham** and described in detail by **Leuwenhock** in 1678. For a long time they were considered parasites. The present knowledge about reproductive physiology is recent, having been derived since thirties.

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